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THE HIGHER CLASSIFICATION,
PHYLOGENY AND ZOOGEOGRAPHY OF
THE SATYRIDAE (LEPIDOPTERA)

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Introduction

The Problem. — The objective of this study, briefly, is the analysis, both in space and, where possible, in time, of the evolution, phylogeny and zoogeography of the higher taxa of the Satyridae. The existing studies on the family have been generally regional, and little progress has been made on interrelating the faunae of the various regions of the world. Furthermore, these studies were not based on modern, multi-variant taxonomic principles; hence, as will be shown, some fundamental errors in relationships have been perpetrated. Since no adequate taxonomic revision of the higher categories of the Satyridae is available, it has been necessary to complete one as a basis for the evolutionary and zoogeographic discussions. Using morphological and distributional data as bases, a scheme for the evolution and zoogeography of the Satyridae is proposed, and finally a phylogeny of the family is projected.

Historical Sketch. — Linné considered all butterflies congeneric. In the Tenth Edition of his *Systema Naturae* (1758), the starting point of zoological nomenclature, he published descriptions of a

number of satyrids, placing them with all other butterflies in the genus
Papilio. The first nomenclatorially valid satyrid genus, *Maniola,* was
erected by Schrank (1801) in his *Fauna Boica.* Fabricius (1807)
described several more genera in Illiger's rare *Magazin für Inseckt-
enkunde.* Latreille (1810) proposed *Satyrus* in his *Considerations
générales sur l'ordre natural des animaux . . . crustacés . . . arach-
nides . . . et insectes . . .* Hübner, between the years 1806 and
1819 (the latter date is bibliographically indeterminate and is brack-
eted in all succeeding references), published many satyrid generic
names in the *Sammlung Exotischer Schmetterlinge* and the *Verzeich-
niss bekannter Schmettlinge* [sic]. Several other authors, notably
Billberg (1820) and Meigen (1829), proposed early generic names
for satyrids, but it was not until 1836 that the family was described,
as "Satyrides", by Boisduval. That author also first proposed the
Brassolinae, as "Brassolides".

The first comprehensive work devoted to the butterflies of the
world in which the treatment was anything like a modern one was
The genera of diurnal Lepidoptera by E. Doubleday, J. O. Westwood
and W. C. Hewitson which appeared in two volumes between 1846
and 1852. In this work the Satyridae were defined, the brassolines
delimited (as a subfamily of the Morphidae) and many generic names
were added to the Satyridae. The practice of separating the brasso-
lines from the rest of the satyrids became firmly established with this
publication. The majority of the satyrid generic names were de-
scribed in this work between 1849 and 1851, after Doubleday's death,
and are usually considered to have been authored by Westwood.
The authors always referred to this work as "Doubleday, Westwood
and Hewitson", even though Hewitson's chief role was as illustrator;
but Brown (1941) holds that text descriptions must be credited to
either Doubleday or Westwood alone, while names first proposed in
plates (the text and the plates were often separately published) should
be credited to Doubleday and Hewitson or to Westwood and Hewit-
son. Accordingly, in those instances where the text appeared simul-
taneously with, or prior to, the plates, I am crediting authorship to
either Doubleday or Westwood, but if the plates appeared before the
text descriptions, credit must be given to Doubleday and Hewitson or
to Westwood and Hewitson.

The first attempt at a higher classification of the satyrids (actually,

of all the butterflies) was that of Herrich-Schäffer (1864). For the first time the satyrids were split beyond the Satyrinae and Brassolinae, as "Satyrina" and "Brassolina". The Biinae ("Biina"), Haeterinae ("Hetaerina" [sic]), Ragadiinae ("Ragadiina") and Elymniinae ("Elymniina") were established. This work has been too long overlooked by systematists — all but one of the presently recognized satyrid subfamilies were defined in it. Röber (1892), in the second volume of Staudinger and Schatz' *Exotische Schmetterlinge,* divided the satyrid genera into six groups with a residue of indeterminate genera. Röber's groups generally correspond to major divisions of the Satyridae, but they were not nomenclatorially designated. Moore in the first and second volumes of his *Lepidoptera Indica,* published between 1890 and 1893, proposed a great many generic names but considered these genera to be apportioned into only the Satyrinae and Elymniinae. These same divisions are to be found in Gaede (1931). The Röber scheme was followed with little modification by Fruhstorfer, Weymer and Aurivillius in their respective sections of Seitz' monumental *Die Grossschmetterlinge der Erde.*

More recently Clark (1947) subdivided the satyrids, exclusive of the brassolines, into the Satyrinae, Enodiinae, Pronophilinae, Elymniinae and Pierellinae (a synonym of Haeterinae). In 1948 he emended Enodiinae to Lethinae and divided the brassolines, as a separate family, into the Brassolinae, Caliginae and Biinae (this last not properly a brassoline). In neither paper did Clark give definitive reasons for his classification, hence he has been criticized by such authors as Ehrlich (1958) who proposed a higher classification of the "true butterflies" (Papilionoidea), retaining the separation of the brassolines and the satyrids and placing the former with the Morphidae.

Table 1 attempts to relate the classifications of Herrich-Schäffer (1864) and Clark (1947, 1948) with that proposed in the present paper. In many instances particular genera were not apportioned by either Herrich-Schäffer or Clark, and those authors' intentions can only be guessed.

With the exception of Clark (1947, 1948) and Ehrlich (1958), no modern author has attempted to place the satyrids in their proper evolutionary positions, and there has been no zoogeographic analysis of this family. Schwanwitsch (1924), however, relied heavily on

TABLE 1

A comparison of the present subfamilial classification of the Satyridae with those proposed by Herrich-Schäffer (1864) and Clark (1947, 1948).

Present classification	Herrich-Schäffer's classification	Clark's classification
Haeterinae	Hetaerina (sic)	Pierellinae
Brassolinae	Brassolina	Brassolinae
		Caliginae
Biinae	Biina	Biinae (of Brassolidae)
	Satyrina (part)	Satyrinae (part)
Elymniinae	Elymniina	Elymniinae
	Satyrina (part)	Enodiinae
		(=Lethinae)
Eritinae	Satyrina	Satyrinae
Ragadiinae	Ragadiina	Satyrinae
Satyrinae	Satyrina	Satyrinae (part)
		Pronophilinae

satyrids in his study of the evolutionary trends toward the development of the "basic nymphalid pattern". This work was followed by a number of other papers concerning pattern modifications, two of which are of interest here: in 1925 he published an analysis of the *Pierella*-type pattern, a paper which has since become a classic in the explanation of the morphological migration of pattern elements; and in 1931 he analyzed the highly modified *Melanargia*-type pattern. Both papers were significant, but the one explaining "pierellization" has had the most far-reaching implications.

Material Studied and Methods Employed. — Since there are between 2500 and 3000 species in the Satyridae, it would be impractical to attempt a complete revision of all the species in a single work. The number of described genera, on the other hand, is manageable — fewer than 400.

A fair axiom in systematics may be stated more or less as follows: *systematic decisions at one taxonomic level should be reached by examination of most (preferably all) of the entities at the next lower major taxonomic level.* In other words, if one is revising a genus, one should see representatives of the species and subspecies included in it to make meaningful taxonomic judgments at the specific and generic levels. In the present study examples of the already-named genera were examined, hence, taxonomic judgments are made at the tribal level, and no synonymization of nomenclatorially valid

genera (only pure objective synonyms) has been attempted, nor have
the several new genera which certainly exist been named. This is
work for careful species-by-species revisions. It is certain that many
of the nomenclatorially valid genera are not biological entities; for
example, I am unable to ascertain any significant differences at the
generic level between the seven nomenclatorially valid genera included
in the satyrine tribe Melanargiini. Nevertheless, all of the nomencla-
torially valid names are carried in this revision.

For the initial work on this project the collection of Carnegie
Museum was examined for representatives of the known genera. It
soon was apparent that the material at hand was not sufficient, so
two months were spent at that Mecca of butterfly systematists, the
British Museum (Natural History), examining those genera which
were either unrepresented at Carnegie Museum or only poorly rep-
resented. Material was found and examined in these collections rep-
resenting all but four of the genera that had come to my attention by
August, 1964. Those genera that have been described since that
time are listed in what I believe to be their proper systematic posi-
tions, but none of them has been examined as critically as have the
others.

Sokal and Sneath (1963: 161-162) explain the "exemplar meth-
od" of taxonomy as follows: a taxon may be characterized by a small
number of entities within it (even a single specimen) because the
variation within taxa is considered to be less than that between taxa.
This is somewhat the method that has been employed in the present
study. The type-species of a genus is considered to be typical of it,
and the various genera are defined chiefly by their type-species in the
following pages. Occasionally the type-species is aberrant, but it is
the type-species which bears nomenclatorial "responsibility" for the
generic name, in any event. Where possible, other species of the
genera were examined, though not in as great detail as the type-
species.

The systematic revision is based entirely upon external morpho-
logical characteristics with many attributes being considered. Wing
venation drawings were made from specimens either with an ocular
grid under a dissecting microscope or with a projection device for
larger specimens. Antennae, palpi, fore-, mid- and hindlegs were re-
moved from the specimen, bleached in clorox and mounted on perma-

nent slides.   Drawings of these structures were made with a camera lucida.

The taxonomic and phylogenetic analysis of the family has been generally based on the premises that (1) entities which more nearly resemble one another in many characteristics are most closely related, (2) structures which are reduced and fused represent advanced conditions (Fox, 1956: 24; Fox and Fox, 1964: 71-72; Brown, 1965) and (3) those organisms which bear advanced characteristics (not just a single advanced character, but several of them) are probably themselves advanced (for example, see Mayr, 1965).   This is in accord with the current paleontological evidence drawn from existing fossil records.

The only taxonomically valuable structures not utilized in this study were the male and female genitalia.   Examination of several regional works (for example, Hayward, 1953; Forster, 1964) shows little reliance can be placed on genitalic structures for classification above the generic level, although these structures are certainly of great importance in specific, and sometimes generic, determination.

Authorship of higher taxa has caused some problems.   According to Art. 36 of the *International Code of Zoological Nomenclature* (1961), the proposition of the family Satyridae by Boisduval (1836, as "Satyrides") implicitly creates also the subfamily Satyrinae and the tribe Satyrini.   It is this rule which has been followed throughout the present paper for the assignment of authorship to the higher taxa.

The zoogeographic analysis has been carried on in light of the principles of vertebrate zoogeography, which is firmly based on and supported by fossil evidence.   For a summary of such evidence see Darlington (1957).   There are too few butterfly fossils to support or refute any zoogeographic statement.   Heavy reliance has been placed on the presence in one area or another of relict, annectant forms: such species may occur nearer the place of origin of the taxon than do others.   Although fossil evidence shows that such groups as horses and rhinoceri evolved more extensively in the Nearctic than in the Palearctic, yet are now absent from the former, many other groups have evolved more or less in the places of their greatest present-day density and diversity.   In the absence of fossil evidence to the contrary, the latter situation is considered to be likely in the satyrid butterflies.

COMPARATIVE MORPHOLOGY

The characters utilized in this study are all external and morphological. Their distribution and evolutionary patterns are given in the following pages.

Antennae. — Four measurements were made on the antennae: the total length; the length of the club, where the club is a discreet entity; the width of the shaft and the width of the club at its thickest point. The antennae of Satyridae demonstrate the tricarinate condition typical of the Nymphaloidea (Fig. 249), although the ridges may not be apparent throughout the entire length of the antennae. The antennae are scaled, but only on the basal few segments in the Haeterinae. In general, the antennal club is not greatly thickened nor flattened at the tip in the primitive satyrids (Figs. 114, 122, 128 which are some of the best developed ones), thereby following the general primitive condition in butterflies. Many of the more advanced Satyrinae, conversely, have the antennal club strongly developed, flattened at the tips and occasionally exhibiting bizarre configurations in some Hypocystini and Pronophilini (Figs. 163, 166, 169, 291, for example). The antennal clubs of other Satyrinae are shown in Figs. 142, 151, 191, 213, 220, 235, 249, 262, 297.

Head. — Three measurements were made on the head region: least intraocular distance; height of the eye and width of the eye. The eyes of all satyrids are entire. Little significance could be gleaned from these measurements, but the eyes of the Satyrinae appear to be more ovoid than those of other subfamilies.

Labial Palpi. — In common with other butterflies the labial palpi of the Satyridae are three-segmented. The basal segment is so firmly attached to the head that it was often broken in dissection, hence is little used in the present study. Five measurements were made on the palpi: the length of the first segment, when it was not broken; the length of the second segment; the length of the third segment; the maximum width of the second segment and the maximum length of the hairs of the second segment. The relationship between the lengths of the second and third segments of the palpi varies, often without regard to phyletic groups. For example, most of the Satyrini display an extremely short third palpal segment, about one-fifth as long as the second, whereas the Pronophilini, which are closely related to the Satyrini and may have been derived from a fairly recent common an-

cestor, show the longest third palpal segment of any satyrid tribe —
in some instances over half as long as the second segment. The sec-
ond segment is generally between five and eight times as long as it is
wide, again with no apparent phylogenetic correlation. The relative
lengths of the hairs of the second segment of the palpi show some in-
teresting trends. In general the hairs are longer in the Satyrinae than
in the other subfamilies, but this tendency is modified in those groups
which have both tropical and temperate or alpine members. In such
instances the relative length of the hairs increases as the altitude or
latitude increases. Examples of the labial palpi of the Satyridae are
shown in many figures in the text, such as Figs. 3, 10, 22, 30, 35, 50,
82, 93, 100, 129, 135, 143, 172, 198, 214, 225, 236, 250, 263,
298, 311.

Thorax. — Only one thoracic measurement was made: the length
of the dorsal thoracic elements. This measurement, unfortunately, is
generally dependent only upon the absolute size of the insect.

Forelegs. — The forelegs of both sexes are more or less reduced
in all satyrids, as in other members of the Nymphaloidea. The fore-
coxae are moveable, as determined by examination of many (though
not all) genera. The forecoxae are not reduced to the extent that the
more distal elements of the forelegs are. The reduction of the pro-
thoracic femur, tibia and tarsus has long been the criterion for re-
garding the Nymphaloidea as the most advanced of the lepidopterous
insects, a concept recently challenged by Ehrlich (1958).

Male forelegs. — Four measurements were made on the male
forelegs: the length of the tarsus; the length of the first tarsal sub-
segment; the length of the tibia and the length of the femur. The
miniaturization of the male forelegs generally follows phylogenetic
lines, being least miniaturized (and reduced; for a discussion of the
terms "miniaturized" and "reduced" see Fox, 1967) in the Haeter-
inae, Brassolinae, Biinae, Elymniinae and Eritinae and most in the
Ragadiinae and Satyrinae (compare the graphs in Figs. 1, 20, 170,
309, for example). In the first five subfamilies the femur, tibia and
tarsus usually are all relatively well developed (an exception is *Cae-
rois,* Fig. 27, where the tibia and the tarsus are much miniaturized).
The foretarsus in these primitive subfamilies is typically monomerous,
but some genera may have up to four freely articulating subsegments.
Examples of the forelegs of typical primitive satyrids are Figs. 4, 11,

23, 51, etc. In the Ragadiinae and Satyrinae the forelegs are much more miniaturized and reduced than in the other five subfamilies, and occasionally there is an apparent total loss of the tarsus (Ypthimini, Fig. 177). The tibia and femur are also greatly miniaturized, but the coxa does not seem affected by this general trend. An anomalous situation exists in the Satyrini and Erebiini, however, where a few genera display great miniaturization of the total foreleg but still retain up to four distinct, though tiny, tarsal subsegments. The male foreleg of *Ragadia* is shown in Fig. 136, and those of representative Satyrinae are shown in Figs. 144, 173, 193, 199, 215, 226, 237, 251, 266, 299, 312, etc.

Female forelegs. — Five measurements were made on the female forelegs: the length of the tarsus; the length of the first tarsal subsegment; the length of the fifth tarsal subsegment, if any was present; the length of the tibia and the length of the femur. The female forelegs potentially show more precise inter- and intrasubfamilial relationships than do those of the males. The forelegs of the Haeterinae, Brassolinae, Biinae and Elymniinae are quite well developed (Figs. 1, 20, 41, 48, 88, 89, 98), always have pentamerous tarsi and usually have posttarsal pulvilli present, except a few of the more advanced Elymniinae. In these families the tarsus is not, or only weakly, clubbed (for example, Figs. 5, 15, 24, 52, 112). In only two genera, *Paralethe* and *Antirrhea* (Fig. 24) are there posttarsal claws, and always there is but a single claw. This represents a more advanced condition generally than that shown in the Ithomiidae (Fox, 1956: 13). The female forelegs of the Eritinae (Figs. 125, 131) and the Ragadiinae (Fig. 137) are miniaturized beyond the point shown in the preceding subfamilies, but they retain the full complement of tarsal subsegments; the tarsus itself is clubbed and not so freely articulated as in the primitive subfamilies. In the Satyrinae the forelegs range from miniaturized, but with five tarsal subsegments, to highly reduced, as much so or more than in the males. Hypocystini, Ypthimini (interestingly where the greatest reduction takes place in the male foreleg), Euptychiini, most Pronophilini and some members of several other tribes have pentamerous tarsi (Figs. 145, 174, 194, 200, 267, for example), but the tarsus is always clubbed. The forelegs of female Satyrini, Melanargiini, Dirini, Coenonymphini and Maniolini are always reduced and apparently lack one or more tarsal

subsegments (Figs. 216, 227, 238, 252, 300, 313, for example).
The miniaturization of the forelegs of Satyrinae through the phyletic
lines may be seen by examination of Figs. 140, 170, 211, 295, 309,
etc.

Walking Legs. — Six measurements were made on both the
mesothoracic and metathoracic legs: the length of the tarsal claws;
the length of the tarsus, exclusive of the claws; the length of the first
tarsal subsegment; the length of the tibia; the length of the tibial spurs,
if any, and the length of the femur. The more important taxonomic
characters are on the mesothoracic legs. The lack of tibial spurs
characterizes the Haeterinae, Biini and Elymniini (Figs. 6, 33, 96),
and these spurs have been lost sporadically in such other groups as
the Ypthimini (Fig. 179) and Coenonymphini (Fig. 221). The
posttarsal claws are bifid in the Melanitini (Fig. 39) and in a few
other genera (*Samanta* and *Manataria,* Fig. 47). In all other Saty-
ridae the claws are simple. The relative lengths of the midtibia and
the first midtarsal subsegment are important taxonomically, particu-
larly within the Satyrinae. Usually the midtibia is between one and
a half and two times as long as the first midtarsal subsegment, but
the midtibia is barely longer than the first tarsal subsegment in the
Satyrini (Fig. 301) and in some Dirini (Fig. 259), whereas the mid-
tibia is always more than twice as long as the basal midtarsal sub-
segment in the Coenonymphini (Fig. 217). All members of the
Satyrus series of the Satyrini display a heavy spine at the dorsal distal
end of the midtibia (Fig. 301), a characteristic weakly shown by
some Dirini (as *Torynesis,* Fig. 259), thereby indicating a close re-
lationship between these two tribes. Dorsal spinosity of the midtibia
is shown by some members of most groups and is characteristic of
others: Haeterinae, Zetherini, Pronophilini, Dirini, Satyrini and Me-
lanargiini.

Examination of the charts of relative lengths of legs shows that
the hindlegs are occasionally significantly longer (Satyrini, Fig. 295,
for example) or shorter (the *Pronophila* series of the Pronophilini,
Fig. 260, for example) than the midlegs, but generally these legs are
subequal.

Wings. — The wings have long been the most-used basis for the
classification of butterflies, both from the aspect of venation and the
distribution of androconial patches. Undoubtedly too much empha-

sis has been placed in the past on wing venation and androconial distribution alone, but it is illogical to ignore the structure of the wings because of previous preoccupation.

Forewings: The following four measurements were made to delimit the shape of the forewing: the length from the base to the end of vein R_5; the length from the base to the end of M_2; the length from the base to the end of 2A and the distance between the end of R_5 and the end of 2A. The cell was delimited by two measurements: from the base to the origins of M_1 and M_3. Five measurements were made to determine the relative positions of the origins of the veins: the distance from the origin of Rs to the origin of M_1; from the origin of M_1 to the origin of M_2; from the origin of M_2 to the origin of M_3; from the origin of M_3 to the origin of Cu_1 and from the origin of Cu_1 to the origin of Cu_2. Inasmuch as the inflation of the forewing veins has long been considered a key characteristic of the Satyridae, the following three measurements were made: the thickest part of Sc; the thickest part of the cubital stem and the thickest part of 2A. In general the longest forewing cell is displayed by the most primitive subfamilies, the Haeterinae (Figs. 2, 7, 8), Brassolinae (Figs. 9, 13, 14, 17, 19) and Biinae (Figs. 21, 26, 28, 29, 34, 40), where the cell is frequently more than three-fifths the length of the wing. In most other groups the cell is about half as long as the wing, but the Elymniini are characterized by an extremely short forewing cell (Figs. 90-92), often less than a third the length of the wing. There appear to be no broad phylogenetic implications shown by the relative placement of the veins along the cell, though several relationships are shown within subfamilies, particularly the proximity of the origins of M_3 and Cu_1 in the Elymniini (Figs. 90-92). The classic definition of the Satyridae includes a statement about the inflation of the stems of the three basic forewing veins. This is simply not diagnostic: the inflation of the veins of *Melanargia* (Fig. 310), for example, is considerably less than that of the true nymphalid genus *Mestra*. Within the Satyridae particular inflation patterns are characteristic: the Mycalesini are characterized by the inflation of all three stems, that of 2A being more or less quadrate (Figs. 99, 104-106, 109, 113, 115, 119); all stems are inflated in the Hypocystini (Figs. 141, 147-150, 156, 161, 162, 165, 167, 168) and Coenonymphini (Figs. 212, 219), but the inflation of 2A is rounded, not quadrate. In contrast, most

Biinae, Ragadiinae, Eritinae and Elymniinae (except the before-mentioned Mycalesini) have relatively uninflated cubital stems and 2A (Figs. 21, 29, 34, 49, 81, 90, 127, 134, for example). The presence of a vestige of forewing vein 3A is characteristic of the Haeterinae (Figs. 2, 7, 8) and seems to connect them with the Ithomiidae.

Hindwings. — Five measurements were made to delineate the shape of the hindwing and account for the majority of "tails": the length from the base to the end of vein Rs; the length from the base to the end of M_3; the length from the base to the end of Cu_2; the length from the base to the end of 2A and the distance from the end of Rs to the end of 2A. The cell was delimited by two measurements: from the base to the origins of M_1 and M_3. Five measurements showed the relative placement of the veins along the cell: from the origin of Rs to the origin of M_1; from the origin of M_1 to the origin of M_2; from the origin of M_2 to the origin of M_3; from the origin of M_3 to the origin of Cu_1 and from the origin of Cu_1 to the origin of Cu_2. In all Satyrinae except Dirini (Figs. 248, 255, 256) the hindwing cell averaged greater than half the length of the wing measured to the end of M_3 (for example, Figs. 141, 171, 197, 212, 224, 234, 261, 296, 310), whereas in the other subfamilies the hindwing cell is half or less the length of the wing, again particularly short in the Elymniini (Figs. 90-92). The actual shape of the cell, which is not reflected in the raw measurements, has some phyletic significance. The cell is distally rounded in the Haeterinae (Figs. 2, 7, 8), perhaps representing a more generalized condition. In the Biinae a gradation may be seen between a rounded cell and one produced at the origins of M_3 and Cu_1 (Figs. 21, 26, 28, 29, 34, 40). The Elymniinae and the "Ypthimini complex" of the Satyrinae, as well as the Eritinae, have the cell produced at the origin of M_3 (Figs. 49, 90, 99, 127, 171, 197, for example), whereas the *Hypocysta* series of the Hypocystini and the "Satyrini complex" of the Satyrinae, in general, display a migration of crossvein m_2-m_3 outward at M_2 and a corresponding blunting of the cell (Figs. 141, 261, 296, 304, for example).

The Ragadiinae (Figs. 134, 139) do not fit another part of the classic definition of the Satyridae — the closure of the cells by tubular veins. In males of this subfamily the hindwing cell is closed by vestigial, non-tubular veins, apparently only for the support of an

androconial patch; some females have the cell completely open.

Because of the migration of crossvein m_2-m_3, M_2 arises nearer to the origin of M_3 than to the origin of M_1 in some satyrine tribes; in other groups M_2 arises somewhat to much nearer M_1. Connate veins are generally considered an advanced characteristic of the Lepidoptera, but in the Satyridae the opposite may be true. Hindwing veins M_3 and Cu_1 are frequently connate in the more primitive subfamilies, particularly the Haeterinae and the Elymniinae (for example, Figs. 2, 60, 90), but these veins are well separated in the Satyrinae (for example, Figs. 261, 296), which are more advanced from a number of other viewpoints, as detailed in the preceding pages. This situation is emphasized chiefly as an illustration of the independence of characters and the danger of reliance on too few attributes, as has been suggested by some authors (for example, Warren, 1947). Hindwing vein R_1 of the hindwing characteristically is basally free in the Brassolinae (Figs. 9, 13, 14, 17, 19) and Elymniini (Figs. 90-92).

Androconial Patches. — As noted previously the distribution of androconial patches has been used extensively in the establishment of genera (particularly by Moore, 1890-1893) — probably to too great an extent. A few general statements may be made concerning the distribution of these patches. There are several sites of the production of androconia on the forewing, the most common of which is the discal area just outside the cell from the inner margin to the origin of M_3. This patch may be highly modified to include all or any part of the area and generally consists of a patch of mealy scales. Hair patches are less frequent on the forewing and are usually restricted to the area below the cubital stem on the upper surface or along 2A on the under surface, particularly in the Biinae and Mycalesini; resultant distortion of the venation may occur in these groups. Several areas generate androconial patches on the hindwing. Mealy patches are generally found near the end of the cell in the area of M_3 (for example, Fig. 54). Hair patches are found in three general areas: above the cell near the origins of Rs and M_1 (for example, Fig. 73), within the cell proper (particularly characteristic of the Elymniini, Figs. 90-92, and Ragadiinae, Figs. 134, 139) and along the anal veins (for example, Fig. 121). Since androconia appear sporadically within most groups they seem to have little phylogenetic signifi-

cance, though particular configurations may be characteristic of a few tribes.

Male Genitalia. — Although these structures have been used extensively by some authors for the establishment of genera (particularly by Forster, 1964), the genitalia are not considered in the present study because of the great variability shown in such genera as have not been split on genitalic grounds. While the genitalia are undoubtedly indispensable for the determination of intrageneric affinities, their unrestricted use as the basis for establishing genera is untenable, partly because doing so creates hierarchical difficulties in that genitalia often do not correlate with other structures, resulting in numerous monotypic genera. Too many monobasic taxa tend to obscure relationships within a larger group.

Systematic Revision of the Genera of the Satyridae

Before meaningful statements may be made concerning evolution, phylogeny and zoogeography, it is necessary to analyze relationships. No usable taxonomy presently exists for the Satyridae; the attempt in the following pages to apportion genera to subfamilies and tribes is designed to fill this need. This classification is based on many characters in the hope that it may more nearly approximate a "natural" classification than have some schemes in the past which were based on one or very few characteristics.

It is the purpose of this revision to define, as closely as possible, the subfamilies and tribes which comprise the Satyridae, as well as to define the family itself. No single character can or should be expected to be diagnostic of an entire group: evolution modifies characters indiscriminately, without regard to "sacred" taxonomic ones. That a single character — or even several — is atypical of the group in some genera is no reason to assign such genera to other tribes (Simpson, 1961a: 54-63). The practice of "splitting" across natural boundaries comes from the indiscriminate analysis of too few characters.

Two other nymphaloid families are considered to be systematically and phylogenetically close to the Satyridae: the Morphidae and the Ithomiidae.

The Morphidae, which are represented in both the Old and New World tropics, have been regarded by many authors (*e.g.,* Ehrlich, 1958) to be very near the Satyridae. With few exceptions the hind-

wing cell of the morphids is open between veins M_2 and M_3, whereas only satyrids of the subfamily Ragadiinae have the cell closed by other than fully functional tubular veins. The structure of the morphid legs is substantially that shown by the primitive satyrids, but larval foodplant preference will separate some morphids. All the Indo-Australian morphids feed as larvae on monocotyledons, as do the satyrids, but the Neotropical members feed predominantly on dicotyledons. There are a few nymphalid genera that utilize monocotyledons, but *Morpho* is unique among nymphaloids in commonly using both monocots and dicots (Ehrlich and Raven, 1965). On the larval foodplant preference and on pattern morphology (see Schwanwitsch, 1924) the New World morphids appear to be very close to the condition apparent when the fundamental dichotomy of the nymphaloids into monocotyledon and dicotyledon feeding groups took place.

Fox (1956: 18-19) considers the Ithomiidae to be as near or nearer the Satyridae than to the Danaidae, with which the ithomiids had formerly been placed. This conclusion was reached from the evidence of various characteristics, particularly of the adults and pupae. In many respects the ithomiids resemble the Haeterinae of the Satyridae, particularly as regards the presence of a vestige of forewing vein 3A (a characteristic also shared with the danaids) in both groups. The obviously similar tendency of the ithomiids and the haeterines to have hyaline wings is, therefore, supported by structural evidence. The vestige of forewing vein 3A will serve to separate the ithomiids from the remainder of the satyrids, and no discreet androconial areas are found in the haeterines, but these are usual (and taxonomically important) in the ithomiids. All Ithomiidae feed as larvae on the dicotyledonous family Solanaceae. The morphids appear to be even more closely related to the satyrids than the ithomiids, but neither can be combined with the satyrids.

Family SATYRIDAE Boisduval, 1836

Satyrides Boisduval, 1836: 166.
= Hipparchiadae Kirby, 1837: 297.
= Satyridae Swainson, 1840: 86.

As mentioned in the preceding section, the Satyridae are related

to the nymphaloid families Morphidae and Ithomiidae.

No single key character will serve to separate the satyrids from all other nymphaloids, but a general definition of the Satyridae may be formulated as follows: a nymphaloid family having a larva with a bifid tail (fleshy anal projections from the eleventh abdominal segment) and feeding on monocotyledonous plants and generally having adults with the cells of the fore- and hindwings closed by tubular veins, forewing veins swollen at their bases and with more or less shaggy palpi. Only the habit of feeding on monocots and the bifid larval tail are universal in the Satyridae, and some morphids feed on monocotyledons. Many other nymphaloids (danaids, ithomiids, acraeines, etc.) have the cells of both wings closed by tubular veins, and the satyrid subfamily Ragadiinae is defined by *not* having the hindwing cell closed by tubular veins, often not closed at all. While many of the satyrids have shaggy palpi, many of the primitive ones have only very short hairs on the palpi. This part of the definition universally applies only to the temperate and arctic species. The forewing veins are usually, but not universally, swollen at their bases. The bases of the forewing veins of such satyrid genera as *Melanitis, Lethe, Oeneis* and *Melanargia* are less swollen than are those of such "true" nymphalid genera as *Mestra, Bolboneura* and *Callicore* (see Schatz and Röber, 1892).

The Satyridae are nearly cosmopolitan, being found wherever butterflies in general are found, except on some oceanic islands. These butterflies, like most others, find their greatest development and proliferation in the tropics, not in the temperate zone as claimed by Ehrlich and Raven, (1965: 589).

Seven subfamilies are recognized in this family. The most primitive of these are the Haeterinae, Brassolinae and Biinae; intermediate are the Elymniinae and Eritinae; the Ragadiinae and Satyrinae are advanced.

In the following pages the individual subfamilies are characterized and diagnoses are provided for the tribes embodying the following parameters: (1) condition of the eyes; (2) relative length of the antennae; (3) characteristics of the antennal club; (4) relative lengths of the second and third segments of the palpus; (5) the development of the hairs of the palpus; (6) the development of the male foreleg; (7) the development of the female foreleg; (8) the relative lengths

TABLE 2

Some diagnostic characters of the subfamilies of the Satyridae.

Character	Haeterinae	Brassolinae	Biinae	Elymniinae	Eritinae	Ragadiinae	Satyrinae
Forewing vein 3A	Basally free	Fused with 2A	Fused with 2A	Fused with 2A	Fused with 2A	Fused with 2A	Fused with 2A
Hindwing cell configuration	Closed and distally rounded	Closed and distally straight	Closed and distally straight	Closed and distally straight	Closed and distally straight	Open, or only closed by aberrant veins	Closed and distally straight or produced at m_2-m_3
Hindwing vein R₁	Anastomosed with Sc	Free basally	Anastomosed with Sc	Anastomosed with Sc, but free basally in Elymniini	Anastomosed with Se	Anastomosed with Sc	Anastomosed with Sc
♀ foretarsus	Pentamerous, unclubbed	Pentamerous, unclubbed	Pentamerous, unclubbed	Pentamerous, unclubbed or weakly so	Pentamerous, weakly clubbed	Pentamerous, clubbed	Fewer than 5 subsegments; if 5 subsegments it is clubbed
♂ foreleg	Not greatly reduced	Not greatly reduced	Not greatly reduced	Not greatly reduced	Variable reduction	Greatly reduced	Greatly reduced
Antenna	Club weak, sealed only at base	Club generally weak, scaled completely	Club generally weak, scaled completely	Club weak, scaled completely	Club weak, sealed completely	Club moderate, scaled completely	Club variable, scaled completely

of the mid- and hindlegs, if significant; (9) the relative lengths of the
midtibia and the first midtarsal subsegment; (10) the presence or ab-
sence of dorsal spinosity on the midtibia; (11) the development of
tibial spurs, if any; (12) the presence or absence of a dorsal, distal
spine at the end of the midtibia; (13) the length and shape of the
forewing cell; (14) the branching pattern of the forewing radial veins;
(15) the relative positions of the origins of forewing veins Rs and
M_1; (16) the relative positions of the forewing medial veins; (17)
the relative positions of forewing veins M_3, Cu_1 and Cu_2; (18) the
patterns of inflation of the forewing vein bases; (19) the length and
shape of the hindwing cell; (20) the relative lengths of hindwing
veins $Sc + R_1$ and 3A; (21) the relative positions of hindwing veins
M_3 and Cu_1; (22) the relative positions of the hindwing medial veins;
and (23) characteristic and aberrant superficial patterns and the dis-
tribution of androconia.

Table 2 gives the character states of certain key characteristics
within the satyrid subfamilies. A key to these subfamilies follows.

Key to the Subfamilies of the Satyridae

1. Hindwing cell open or closed only by aberrantly placed veins (Figs. 134,
   139) .... Ragadiinae
   Hindwing cell closed by tubular veins (Fig. 2, for example) 2
2. Forewing with a vestige of vein 3A at base (Figs. 2, 7, 8) ...... Haeterinae
   Forewing vein 3A fused with 2A throughout its entire length (Fig. 21, for
   example) 3
3. Hindwing vein R_1 free basally from $Sc + R_1$ (Figs. 9, 90, for example) 4
   Hindwing vein R_1 completely fused with Sc (Fig. 21, for example) 5
4. Forewing cell greater than half length of wing; Neotropical species ....
   .... Brassolinae
   Forewing cell much less than half length of wing; Paleotropical species ....
   .... Elymniinae (Elymniini)
5. Posttarsal claws bifid (Figs. 39, 47) 6
   Posttarsal claws simple 7
6. Forewing cell more than half length of wing .... Biinae (Melanitini)
   Forewing cell less than half length of wing ....
   .... Elymniinae (*Samanta*) and *Manataria*
7. Female foretarsus with fewer than five subsegments .... many Satyrinae
   Female foretarsus with five subsegments 8
8. Female foretarsus strongly clubbed distad (Fig. 174, for example) ....
   .... many Satyrinae
   Female foretarsus not so clubbed (Figs. 24, 52, 124, for example) 9

9. Forewing cell half length of wing or less .... most Elymniinae
   Forewing cell greater than half length of wing 10
10. Forewing cell produced at the origin of M_3 (Figs. 21, 29, for example);
   New World species .... New World Biinae
   Forewing cell produced at the origin of M_1 (Figs. 121, 127); Indo-Aus-
   tralian species .... Eritinae

Subfamily HAETERINAE Herrich-Schäffer, 1864

Hetaerina [sic] Herrich-Schäffer, 1864: 124.
= Pierellinae Clark, 1947: 149.

The Haeterinae on several counts are the most primitive of the Satyridae. These butterflies cannot be considered close to any other subfamily but show more affinities (albeit slight ones) with the Biinae than with the Brassolinae or Elymniinae. From several aspects — the free proximal end of forewing vein 3A, the general elongate wing form, the seta-like modification of the wing scales and the preference for a deep forest habitat — this subfamily seems to form a connecting link with the Ithomiidae (Fox, 1956: 18-19), but, again, this is a very remote relationship, if not a completely spurious one arising from ecological adaptations.

In itself the free proximal vestige of forewing vein 3A serves to distinguish the haeterines from all other satyrids. This characteristic is otherwise shown in the Nymphaloidea by the Ithomiidae, Danaidae, some Morphidae (*Taenaris*) and such nymphalid genera as *Colaenis, Kallima, Apaturina* and the very primitive *Callinaga*. The general shape of the wings (Figs. 2, 7, 8) is characteristic, as is the rounded hindwing cell. The combination of a dorsally spinose midtibia and the lack of tibial spurs (Fig. 6) is shown by no other satyrid. The lack of distal scaling on the antennae is also peculiar to the present subfamily.

All members of the Haeterinae are restricted to the American tropics and are found only in the dense forests.

A single tribe, the Haeterini, includes all members of the subfamily.

The most comprehensive revision of the Haeterinae presently available is that of Brown (1942).

Tribe HAETERINI Herrich-Schäffer, 1864
(Figures 1-8)

Hetaerina [sic] Herrich-Schäffer, 1864: 124.
= Pierellinae Clark, 1947: 149.

The diagnostic features of this tribe are those outlined for the subfamily above. The Haeterini are characterized as follows:

The eyes are naked. The antennae vary little in length from slightly over one-third (*Pierella*) to just over two-fifths (*Haetera*) the length of the forewing costa. The antennal club is weakly developed, generally less than twice the thickness of the shaft and occupying the distal one-fourth to one-fifth of the antenna. The antennae of the haeterines are scaled on only the proximal few segments: the antennae of all other satyrids are fully scaled. The third segment of the palpus is usually less than one-fifth the length of the second, although the third segment is between one-third and one-fourth the length of the second in *Haetera* and *Pseudohaetera*. The hairs on the second segment of the palpus are generally about as long as the segment is wide (the hairs are twice as long as the segment is wide in *Dulcedo*).
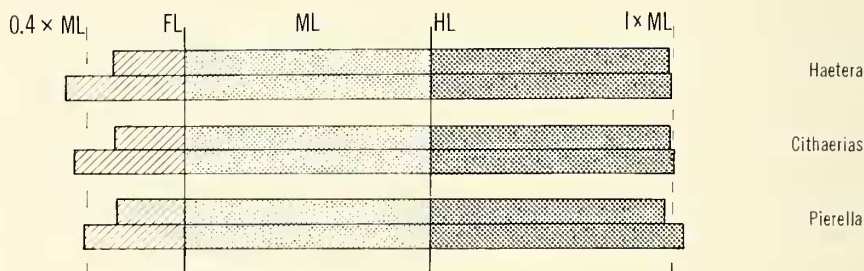
Fig. 1. Haeterinae: Haeterini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

The male foreleg is well developed for a nymphaloid, the tibia is longer than the femur, although both are about equal in *Pierella*, and there is a single, unspined tarsal subsegment in all genera. The female foreleg is also well developed with a pentamerous, unclubbed tarsus
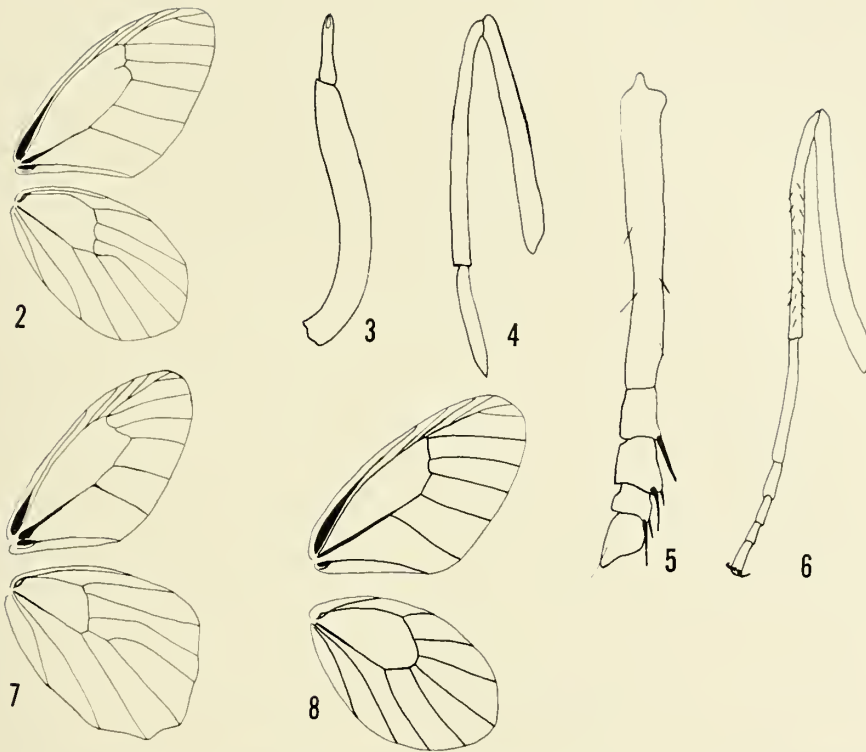
Figs. 2-8. Haeterinae: Haeterini. 2. *Haetera piera* (Linné), ♂ venation. 3. *H. piera*, palpus (in this and all succeeding illustrations of palpi only the distal two segments are figured). 4. *H. piera*, ♂ foreleg (in this and all succeeding illustrations of the ♂ forelegs, unless otherwise indicated, the femur, tibia and tarsus are figured. 5. *H. piera*, ♀ foretarsus. 6. *H. piera*, midleg (in this and all succeeding illustrations of the midlegs only the femur, tibia and tarsus are figured). 7. *Pierella nereis* (Drury), ♂ venation. 8. *Cithaerias pireta* (Cramer), ♂ venation.

armed with spines on the second, third and fourth subsegments. The mid- and hindlegs are of about equal length. The midtibia is one and one-half to two times as long as the first midtarsal subsegment, is spiny dorsad and lacks tibial spurs or a spine at the dorsal, distal end. The relative development of the legs is shown in Fig. 1.

The forewing cell varies from just greater than half to more than three-fifths the length of the forewing costa and is rounded distad in all genera. The forewing radial veins arise in three branches from the cell. Forewing veins Rs and M_1 are connate or approximate at

their origins, vein M_2 arises midway between M_1 and M_3 and vein Cu_1 arises midway between M_3 and Cu_2, or slightly nearer the former. The forewing vein Sc is inflated in all genera, and the other veins may be: both the cubital stem and 2A in *Pierella*, only 2A in *Haetera*. The presence of a proximal vestige of forewing vein 3A is diagnostic in the Haeterinae.

The hindwing cell is also distally rounded and is from two-fifths (*Pierella*) to three-fifths (*Cithaerias*) as long as the wing, as measured to the origin and end of M_3, respectively. Hindwing veins $Sc + R_1$ and 3A are of about the same length. The origins of hindwing veins M_3 and Cu_1 may be widely separated (*Cithaerias*, Fig. 8) to connate on a common stalk (*Pierella*, Fig. 7). Vein M_2 arises about midway between M_1 and M_3, or slightly nearer the latter.

The pattern is distinctive (see Schwanwitsch, 1925): the scales of most species are reduced to narrow, hairlike vestiges, resulting in a hyaline or translucent appearance in most species. Relatively unmodified scales are displayed by some species, particularly of the genera *Pierella* and *Haetera*, with resultant opaque wings.

Genera Included in the Haeterini

Callitaera Butler, 1868b: 101. Type-species: "*Papilio aurora* Felder" (= *Cithaerias phantoma* Fassl, *fide* Clifton, *in litt.*), designated by Brown, 1942: 311.

Cithaerias Hübner, [1819] (1816-1826): 53. Type-species: "*Papilio andromeda* Fabricius" (= *Papilio pireta* Cramer, according to Brown, 1942), designated by Scudder, 1875a: 143. *Papilio menander* Drury, often regarded as the type-species, was shown by d'Almeida (1951: 496) to be identical with *Papilio pireta* Cramer.

Dulcedo d'Almeida, 1951: 501. Type-species: *Haetera polita* Hewitson, by original designation.

Haetera Fabricius, 1807: 284. Type-species: *Papilio piera* Linné, designated by Butler, 1868a: 195.

    = *Oreas* Hübner, [1807] (1806-1838): pl. [82]. Type-species: *Papilio piera* Linné, by monotypy. *Oreas* is sunk to *Haetera* Fabricius in accordance with Opinion 137 (1942) of the International Commission of Zoological Nomenclature.

Pierella Herrich-Schäffer, 1865: 65. Type-species: *Papilio nereis* Drury, designated by Butler, 1868a: 195.

Pseudohaetera Brown, 1942: 330. Type-species: *Haetera hypaesia* Hewitson, by original designation.

Subfamily BRASSOLINAE Boisduval, 1836

Brassolides Boisduval, 1836: 166.

The brassolines have long been considered a separate family somewhat intermediate between the satyrids and the morphids, but Ehrlich (1958: 351-352) placed the brassolines with the morphids. There is little except the large size of the butterflies to support this combination: the larvae of most Neotropical morphids feed on dicots, whereas the brassolines feed exclusively on monocots; brassoline larvae have bifid tails, but the tails are greatly reduced in the morphids. These two characters intimately associate the brassolines with the other satyrids. The cells of both wings are closed in the brassolines, as in the satyrids generally, whereas the hindwing cell is open in most of the Morphidae. Within the Satyridae the brassolines are allied to the New World Biinae, particularly through such genera as *Narope*. There seems little justification, in view of the above facts, for retaining the brassolines as a family separate from the Satyridae.

The brassolines may be distinguished from all other New World Satyridae by the basal separation of hindwing veins Sc and R_1 (Figs. 9, 13, 14, 17, 19). This characteristic is also shown by the Old World Elymniini (Elymniinae), but the extremely short cell and virtually connate veins M_3 and Cu_1 of the forewing immediately distinguishes the elymniines. The Haeterinae show an approximate condition of hindwing veins $Sc + R_1$ and Rs, but there is no basal separation of R_1. The brassolines lack the vestige of forewing vein 3A which characterizes the Haeterinae.

All brassolines are Neotropical, none being found further north than southern Mexico. Some species of *Caligo* are banana pests in Central America, and around the banana plantations these insects often may be seen flying just at dusk.

Clark (1947, 1948) recognized two tribes as subfamilies of "Brassolidae", but no good evidence is found for splitting the brassolines into more than a single tribe, the Brassolini. Within the Brassolini groupings are possible, but not tribal ones.

Tribe BRASSOLINI Boisduval, 1836
(Figures 9-19)

Brassolides Boisduval, 1836: 166.
= Caliginae Clark, 1947: 149.
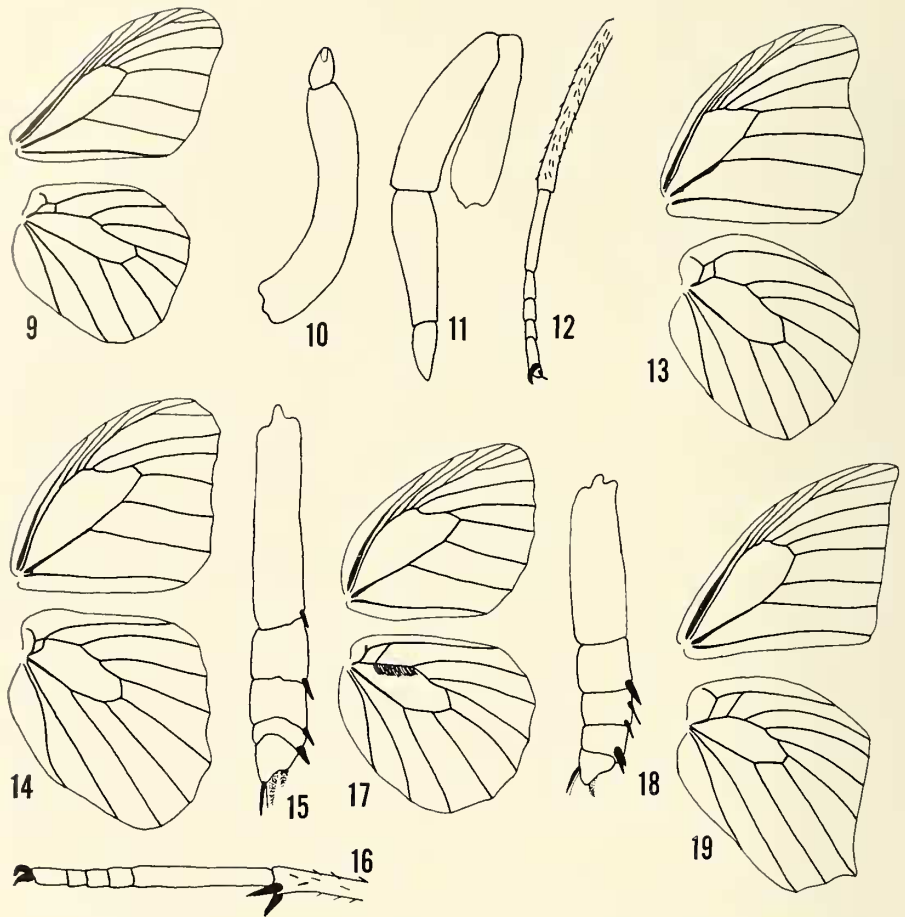
Figs. 9-19. Brassolinae: Brassolini. 9. *Brassolis sophorae* (Linné), ♂
venation. 10. *B. sophorae*, palpus. 11. *B. sophorae*, ♂ foreleg. 12. *B. so-
phorae*, midleg. 13. *Opsiphanes cassiae* (Linné), ♂ venation (after Schatz
and Röber, 1892). 14. *Caligo atreus* Kollar, ♂ venation (after Schatz and
Röber, 1892). 15. *C. eurylochus* (Cramer), ♀ foretarsus. 16. *C. eurylochus*,
midtarsus and distal portion of midtibia. 17. *Dasyophthalma rusina* (Godart),
♂ venation. 18. *D. rusina*, ♀ foretarsus. 19. *Narope cyllastros* Doubleday
and Hewitson, ♂ venation.

The characteristics of the subfamily are those of the tribe. Four
groups may be noted within the tribe, but they are only loose as-
semblages and tend to grade into one another. The diagnostic char-
acters are summarized in Table 3.

The *Brassolis*-series, *sensu stricto,* is composed of robust species with naked eyes, moderately well developed or absent tibial spurs and a basically brown upper surface with a transverse band of orange, yellow or red across the forewing.

The *Caligo*-series includes large, broad-winged, but not robust-bodied butterflies with naked eyes, well developed tibial spurs and a basically iridescent purple upper surface with faint longitudinal light markings.

The *Dasyophthalma*-series is comprised of a single genus of broad-winged species with hairy eyes, moderately well developed tibial spurs and a basically brown upper surface, with or without iridescence, and with longitudinal lighter markings.

The *Narope*-series is also comprised of a single genus of medium-sized butterflies with acute forewing costal margins, naked eyes, moderately well developed tibial spurs and a brown upper surface with little or no maculation.

TABLE 3

The character states of four characters in the genera of the Brassolinae: Brassolini.

Genus	Eyes	Antennal club	Tibial spurs	Length of fore-wing cell/ length of forewing costa
Brassolis-series, s. str.				
Brassolis	Naked	Pronounced	Present, ex. *B. sophorae*	3/5-2/3
Catoblepia	Naked	Gradual	Present	3/5-2/3
Dynastor	Naked	Gradual	Present	1/2-3/5
Opoptera	Naked	Gradual	Present	3/5-2/3
Opsiphanes	Naked	Gradual	Present	1/2-3/5
Penetes	Naked	Gradual	Present	3/5-2/3
Selenophanes	Naked	Gradual	Present	3/5-2/3
Caligo-series				
Caligo	Naked	Gradual	Present	3/5-2/3
Eryphanis	Naked	Gradual	Present	3/5-2/3
Dasyophthalma-series				
Dasyophthalma	Hairy	Gradual	Present	3/5-2/3
Narope-series				
Narope	Naked	Gradual	Present	just >1/2

The Brassolini are characterized as follows. — The eyes are naked in all genera but *Dasyophthalma* in which they are densely hairy. The antennae are short, one-third to two-fifths the length of the forewing costa, and the antennal club is weakly developed in most genera (just over twice the width of the shaft in *Brassolis*). The third segment of the palpus is generally one-fourth to one-sixth the length of the second, although it is far shorter in such rather advanced genera as *Brassolis* and *Opsiphanes* and somewhat longer in the more primitive *Narope*. The hairs of the second segment of the palpus are generally shorter than the segment is wide.

The male foreleg is well-developed with a mono- to trimerous tarsus; the femur is longer than the tibia in all genera. The female foreleg is likewise well developed with a pentamerous, unclubbed tarsus bearing spines on at least the third and fourth (often the first and second, too) subsegments. The midtibia varies from just less than twice (*Caligo* and *Eryphanis*) to well over twice (*Brassolis*-series) as long as the proximal midtarsal subsegment. The midtibia is spiny dorsad with well to moderately well developed tibial spurs (except in *Brassolis sophorae*, where the tibial spurs are totally wanting, Fig. 12); there is no spine at the dorsal, distal end of the midtibia.

The forewing cell is produced at the origin of M_3, particularly in *Caligo* and *Eryphanis*. The cell is generally three-fifths to two-thirds the length of the forewing costa, although it is somewhat shorter in *Dynastor, Opsiphanes* and *Narope*. The forewing radial veins arise from the cell in three branches. Forewing veins Rs and M_1 are well separated at their origins; vein M_2 usually arises nearer M_1 than M_3, although M_2 arises nearer M_3 in *Caligo* and *Dynastor*; vein Cu_1 arises nearer M_3 than Cu_2, except in *Dasyophthalma*. The forewing veins are seldom inflated, though the base of Sc may be in some genera.

The hindwing cell is produced marginad by a migration of crossvein m_2-m_3 and is generally about three-fifths the length of the wing, measured to the origin and the end of M_3, respectively. Hindwing veins Sc and R_1 are separate proximally in this tribe, as in the Elymniini (Elymniinae); Sc + R_1 is longer than 3A. At their origins veins M_3 and Cu_1 are well separated, and M_2 arises nearer M_3 than M_1.

The upper surface patterns have been described in the analysis of the generic series. On the under surface the wings are cryptically patterned, light brown with darker striations, much as in the Antir-

rhini. In the brassolines, however, there are often large "eye-spots", particularly on the hindwing, which have been credited with being protective markings (the wings are rapidly opened when the butterfly is threatened by a predator, giving the impression of large eyes blinking). The development of these eye-spots gives the common name of the *Caligo*-series, the "owl butterflies".

Genera Included in the Brassolini

The *Brassolis*-series, *sensu stricto*

Brassolis Fabricius, 1807: 282. Type-species: *Papilio sophorae* Linné, designated by Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852: 341.

Catoblepia Stichel, 1902: 488, 491. Type-species: *Brassolis amphiroe* Hübner, by original designation.

Dynastor Westwood and Hewitson, 1849, *in* Doubleday, Westwood and Hewitson, 1846-1852: pl. 58. Type-species: *Dynastor napoleon* Westwood and Hewitson, by monotypy.

Opoptera Aurivillius, 1882: 75. Type-species: *Brassolis syme* Hübner, by original designation.

Opsiphanes Westwood and Hewitson, 1849, *in* Doubleday, Westwood and Hewitson, 1846-1852: pl. 57. Type-species: *Opsiphanes sallei* Westwood and Hewitson, designated by Scudder, 1875a: 233.

Penetes Westwood and Hewitson, 1849, *in* Doubleday, Westwood and Hewitson, 1846-1852: pl. 58. Type-species: *Penetes pamphanis* Westwood and Hewitson, by monotypy.

Selenophanes Staudinger, 1888: 212. Type-species: *Papilio cassiope* Cramer, by original designation.

The *Caligo*-series

Caligo Hübner, [1819] (1816-1826): 51. Type-species: *Caligo eurylochus* Hübner, designated by Scudder, 1875a: 129.

Eryphanis Boisduval, 1870: 57. Type-species: *Papilio automedon* Cramer, by monotypy.

Dasyophthalma-series

Dasyophthalma Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852: 343. Type-species: *Brassolis rusina* Godart, designated by Scudder, 1875a: 155.

Narope-series

Narope Westwood and Hewitson, 1849, *in* Doubleday, Westwood and Hewit-
    son, 1846-1852: pl. 50. Type-species: *Narope cyllastros* Westwood
    and Hewitson, by monotypy.

Subfamily BIINAE Herrich-Schäffer, 1864

Biina Herrich-Schäffer, 1864: 124.

The Biinae are the third of the very primitive satyrid groups and
show no especially close relationship with any other subfamily.   The
Neotropical biines share some vague affinities with the haeterines and
some firmer ones with the brassolines, particularly as regards vena-
tion, whereas the Paleotropical biines grade toward the Lethini of the
next subfamily.

The biines are generally large to very large satyrids, often brightly
colored above and always cryptically patterned beneath with few and
usually poorly developed eye-spots on either wing surface.   The long
forewing cell, generally three-fifths the length of the wing except in
some melanitines (Fig. 34), is characteristic, and the well separated
hindwing veins M_3 and Cu_1 serve to distinguish these butterflies from
most elymniines.   The wings are never translucent or transparent, as
in the haeterines.

TABLE 4

Some of the diagnostic characters of the tribes of the Biinae.

Character	Antirrhini	Biini	Melanitini
Tarsal claws	Simple	Simple	Bifid
Tibial spurs	Present, but poorly devel- oped	Absent	Present
Length of 3rd seg. of palpus relative to length of second	<1/4	>1/2	1/4
Forewing radial veins	3 branches	1 branch, aberrant	3 branches
Inflation of forewing veins	Only Sc, if any; or else v. slight	Sc, Cu, 2A greatly inflated	Only Sc, slight

All biines are tropical. The Antirrhini and Biini are found exclusively in the Neotropics and are forest dwellers, whereas the Melanitini are Paleotropical (from West Africa to Australia) and are found in less dense situations, though many of these species are crepuscular.

The Biinae are split, somewhat reluctantly, into three tribes, but *Bia* is far too aberrant to be referred to either of the other two. The diagnostic features of the three tribes are given in Table 4, and a key to these tribes is given below.

KEY TO THE TRIBES OF THE BIINAE

1. Tarsal claws bifid (Fig. 39); Paleotropical species .... Melanitini
   Tarsal claws simple; Neotropical species 2
2. Tibial spurs present, though poorly developed (Fig. 25); third segment of
     palpus less than one-fourth length of second segment (Fig. 22) ....
     .... Antirrhini
   Tibial spurs absent (Fig. 33); third segment of palpus greater than half
     length of second segment (Fig. 30) .... Biini

The New World members of the Biinae are considered to be more primitive because of (1) their greater convergence toward the Brassolinae and Haeterinae, (2) the greater relative size of the male foreleg and (3) the unclubbed female foreleg. The Melanitini are the more advanced members of the subfamily and seem to show relationships with the more advanced Elymniinae.

Tribe ANTIRRHINI, new tribe
(Figures 20-28)

The simple tarsal claws serve to separate this New World tribe from the Old World Melanitini. Many characteristics serve to separate the Antirrhini from the Biini, notably the presence of tibial spurs, the more reduced third segment of the palpus, the arising of the forewing radial veins in three branches and the relative placement of several other veins on the cells.

The Antirrhini are Neotropical insects, found from Guatemala to Paraguay and northern Argentina. All seem to be forest species, seldom venturing into open areas. The tribe Antirrhini is characterized as follows:

The eyes are naked in all genera but *Sinarista,* in which they are sparsely hairy. The antennae are about half as long as the forewing
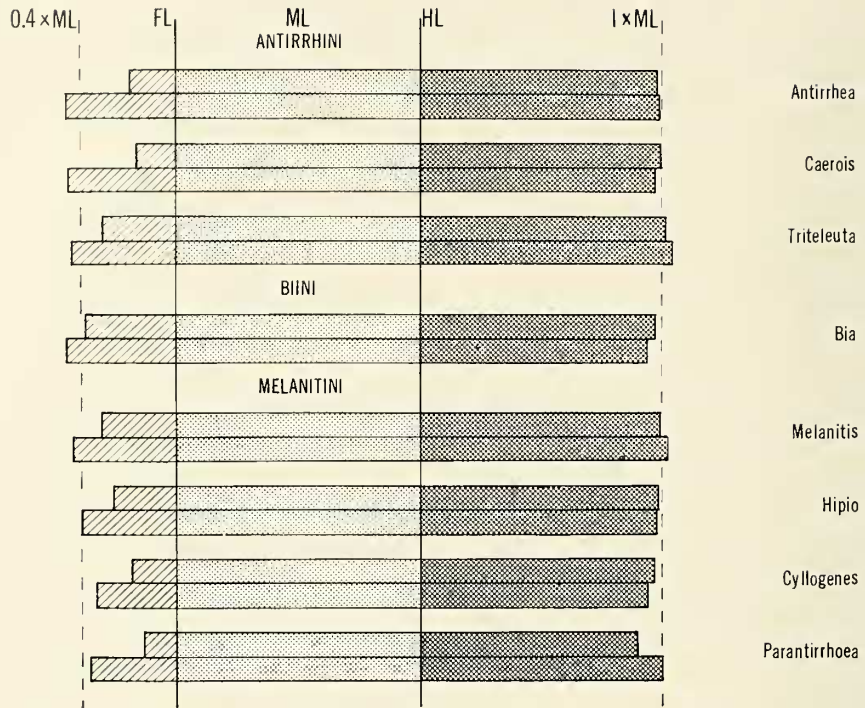
Fig. 20. Biinae: Antirrhini, Biini and Melanitini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

costa, and the antennal club is weakly developed (it is completely indistinct in *Triteleuta*). When the club is distinct it occupies the distal one-third to one-quarter of the antenna and is seldom more than twice as thick as the shaft. The third segment of the palpus is one-fourth to one-sixth the length of the second segment, and the hairs of the second segment are about as long as the segment is wide, although the hairs of *Sinarista* are about twice as long as the width of the segment.

The male foreleg is well developed with a monomerous, unspined tarsus, and the tibia is usually slightly longer than the femur, although the femur is much longer in *Caerois*. The female foreleg is also well developed with a pentamerous, unclubbed tarsus bearing spines on the first four subsegments. The midtibia is more than twice as long

as the basal midtarsal subsegment, smooth dorsally and bearing weakly developed tibial spurs. There is no spine at the dorsal, distal end of the midtibia. The relative lengths of the legs are shown in Fig. 20.

The forewing cell is square-cut in *Caerois* and *Sinarista,* but deeply excavate at M_1 in the other genera. The cell is about three-fifths the length of the forewing costa. The radial veins arise in three branches from the forewing cell, and veins Rs and M_1 are connate to approximate at their origins. Forewing vein M_2 arises midway between M_1 and M_3, whereas Cu_1 usually arises about midway between M_3 and Cu_2 (nearer M_3 in *Caerois*). The forewing veins are only slightly inflated, if at all; any thickening is at the base of Sc.

The hindwing cell is highly variable, from very short and narrow in *Antirrhea* to over three-fifths the length of the wing, measured to the end of M_3, and rounded in *Caerois*. Hindwing vein $Sc + R_1$ is usually longer than 3A, although the two veins are of about the same length in *Sinarista*. Hindwing veins M_3 and Cu_1 are generally well separated at their origins, but they are approximate in *Antirrhea*; vein M_2 arises midway between M_1 and M_3.

Most of the species are rather brightly colored above with few ocelli, although some species, such as *Sinarista adoptiva* Weymer, have rows of submarginal ocelli. On the under surface all species are cryptically marked with many fine, dark striations on a tan to brown ground color. There are androconial hair patches on the under surface of the forewing along vein 2A in all genera but *Sinarista,* and these androconial areas frequently result in distortions of the venation.

Genera Included in the Antirrhini

Antirrhea Hübner, [1822] (1806-1838): pl. 294. Type-species: *Antirrhea archaea* Hübner, by monotypy.
    = *Anchiphlebia* Butler, 1868b: 106. Type-species: *Antirrhea archaea* Hübner, by original designation.

Caerois Hübner, [1819] (1816-1826): 56. Type-species: *Papilio arcesilaus* Cramer (= *Papilio chorinaeus* Fabricius), by monotypy.
    = *Arpidea* Duncan, 1837: 180. Type-species: *Papilio chorinaeus* Fabricius, by monotypy.

Sinarista Weymer, 1909: 164. Type-species: *Sinarista adoptiva* Weymer, by monotypy.

Triteleuta Strand, 1912: 44. Type-species: *Antirrhea tomasia* Butler, by original designation. Proposed as a subgenus of *Antirrhea* Hübner.
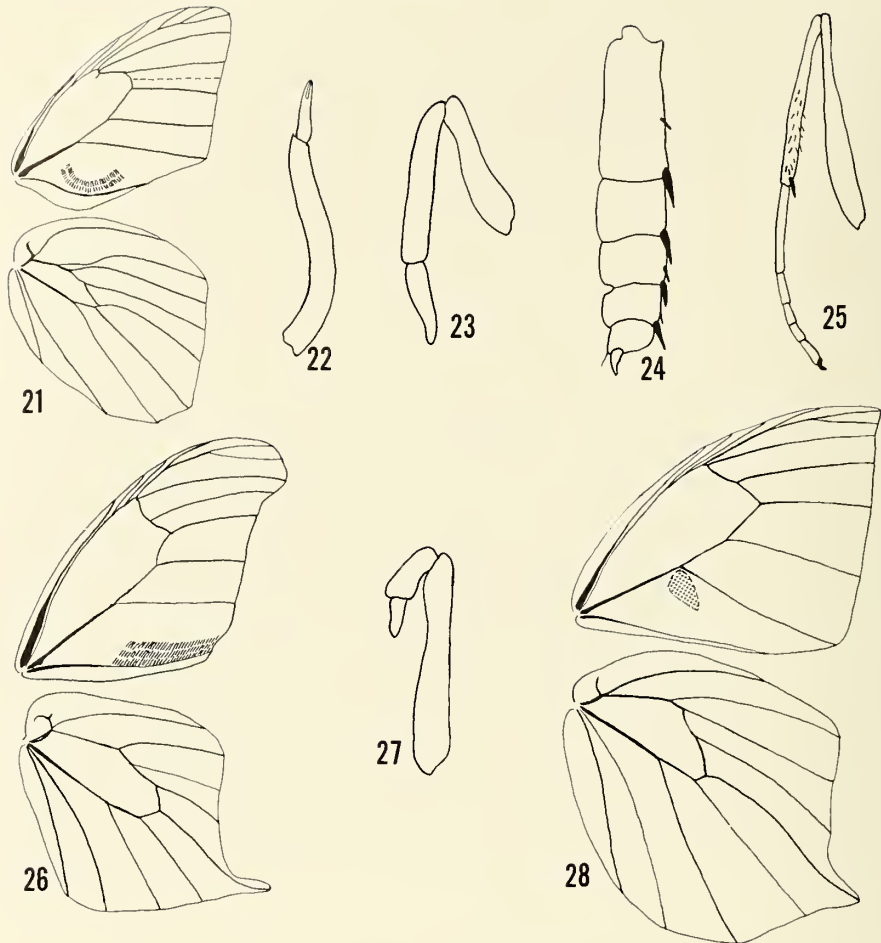
Figs. 21-28. Biinae: Antirrhini. 21. *Antirrhea archaea* Hübner, ♂ vena-
tion. 22. *A. archaea,* palpus. 23. *A. archaea,* ♂ foreleg. 24. *A. archaea,* ♀
foretarsus. 25. *A. archaea,* midleg. 26. *Caerois chorinaeus* (Fabricius), ♂
venation. 27. *C. chorinaeus,* ♂ foreleg. 28. *Sinarista adoptiva* Weymer, ♂
venation.

Tribe Biini Herrich-Schäffer, 1864
(Figures 20, 29-33)

Biina Herrich-Schäffer, 1864: 124.

Bia actoriaena (Linné), the only species included in the Biini, is
the most aberrant member of the Satyridae. It has been considered
variously a brassoline (Weymer, 1912; Clark, 1947, 1948) or a per-
fectly good satyrid (Röber, 1892; Ehrlich, 1958). *Bia* is definitely

a satyrid and shows relationships to other members of the Biinae, chiefly through pattern convergence, but it is far too aberrant to be included in either of the other two biine tribes. This species can be distinguished from all other biines by the lack of tibial spurs, in addition to a multitude of other characteristics enumerated below in the description of the tribe. *Bia* is primitive, though highly specialized, and may be characterized as follows:

The eyes are naked. The antennae are half as long as the forewing costa, and the club is poorly developed occupying the distal quarter of the antenna and about twice as thick as the shaft. The third segment of the palpus is very long, over half the length of the second segment, and the hairs of the second segment are not as long as the segment is wide.

The male foreleg is well developed, with the femur longer than the tibia and a monomerous, unspined tarsus. The female foreleg is also well developed with a pentamerous, unclubbed tarsus bearing spines on the first four subsegments. The midtibia is smooth dorsally, more than twice as long as the proximal midtarsal subsegment and armed with neither tibial spurs nor a spine at the dorsal, distal end.

The forewing cell, measured to the origin of M_3, is greater than three-fifths the length of the forewing costa, but the cell is deeply excavate at the origins of M_1 and M_2, and the cell is only about half the length of the forewing costa when it is measured to the origin of M_1. All the forewing radial veins arise from a single branch from the cell, and R_1 anastomoses distally with Sc, resulting in a confused venational pattern along the costa. Forewing veins Rs and M_1 are well separated at their origins. Vein M_2 arises much nearer M_1 than M_3, whereas Cu_1 arises midway between M_3 and Cu_2. Veins Sc, the cubital stem and 2A are all strongly inflated at their bases, the inflation of the latter suggesting the pattern shown in the Mycalesini of the next subfamily.

The hindwing cell is strongly produced at the origin of M_3 and about three-fifths the length of the wing measured to the end of M_3. Hindwing vein $Sc + R_1$ is longer than 3A. Veins M_3 and Cu_1 are well separated at their origins, and M_2 arises nearer M_1 than M_3.

The upper surface is dark brown with patches of orange and iridescent blue scales. On the under surface *Bia* is marked like other members of the subfamily: tan with numerous, longitudinal brown
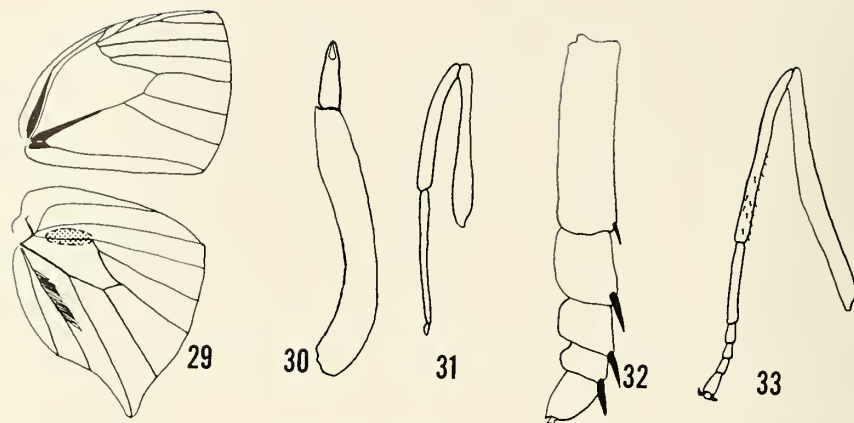
Figs. 29-33.   Biinae: Biini, all *Bia actoriaena* (Linné).   29. ♂ venation.
30. palpus.   31. ♂ foreleg.   32. ♀ foretarsus.   33. midleg.

striae.   The androconial areas on the hindwing are characteristic:
there is a patch of mealy scales on the upper end of the cell along
crossvein r_s-m_1, and a long hair tuft lies along 2A.

Genus Included in the Biini

Bia Hübner, [1819] (1816-1826): 51.   Type-species: *Papilio actoriaena* Linné,
    by monotypy.

Tribe MELANITINI, new tribe
(Figures 20, 34-40)

The melanitines are the most advanced members of the Biinae, as
noted above, particularly with regard to the more reduced male fore-
leg and the slightly clubbed female foretarsus (Fig. 37).   There are,
in addition to the already-mentioned affinities to the Antirrhini, some
rather suggestive ties between the Melanitini and the Lethini of the
next subfamily, especially through the genera *Parantirrhoea* (Mela-
nitini) and *Ptychandra* and *Samanta* (Lethini).   The venation of
Ptychandra and its pattern relate rather closely (but with modifica-
tions) to those of the Melanitini, and *Samanta* displays the bifid claws
characteristic of the melanitines.   Bifid claws are the most character-
istic feature of this tribe and serve to distinguish it from all other
satyrids except *Samanta* and *Manataria* (a Neotropical genus of un-
certain position).

All members of this tribe are Paleotropical, being found from West Africa through the Malay Peninsula east as far as New Guinea and northern Australia. At least some of the species are crepuscular, and they do not appear to be so limited to the deep forest as are the Neotropical Antirrhini. The Melanitini are characterized as follows:

The eyes are naked. The antennae are rather uniformly just over two-fifths the length of the forewing costa, and the antennal club is weakly developed, occupies the distal quarter of the antenna and is thickened twice to two and a half times the thickness of the shaft. The third segment of the palpus is about one-fourth the length of the second, and the hairs of the second segment are much shorter than the segment is wide.
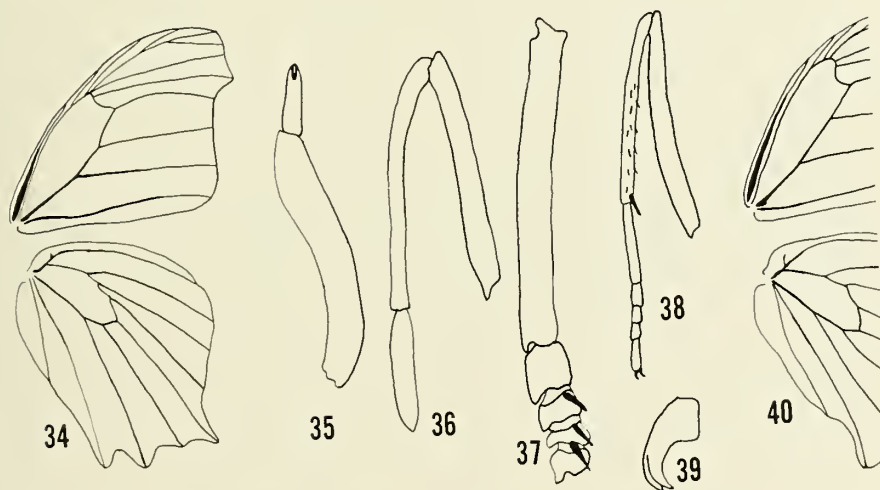
Figs. 34-40. Biinae: Melanitini. 34. *Melanitis leda* (Linné), ♂ venation. 35. *M. leda,* palpus. 36. *M. leda,* ♂ foreleg. 37. *M. leda,* ♀ foretarsus. 38. *M. leda,* midleg. 39. *M. leda,* bifid tarsal claw. 40. *Hipio constantia* (Cramer), venation of proximal portion of ♂ wings.

The male foreleg is well developed with the femur and the tibia of about the same length (the femur is longer in *Cyllogenes* and *Parantirrhoea*) and bearing a single, usually unspined (weakly so in *Cyllogenes*) tarsal subsegment. The female foreleg is also well developed with a pentamerous, unclubbed or weakly clubbed tarsus. The fourth tarsal subsegment always bears spines, and the spines are

present on the third and fourth subsegments in *Gnophodes* and *Par-antirrhoea,* on the second, third and fourth in *Melanitis* and *Hipio.* The midtibia is greater than twice as long as the proximal midtarsal subsegment, is smooth dorsad and bears moderately well developed tibial spurs but no spine at the dorsal, distal end. Relative lengths of legs are shown in Fig. 20.

The forewing cell varies from just over half to nearly three-fifths as long as the forewing costa and is somewhat excavate at m_2-m_3. The forewing radial veins arise in three branches. Veins Rs and M_1 are usually well separated at their origins, vein M_2 arises much closer to M_1 than to M_3 and Cu_1 usually arises midway between M_3 and Cu_2, although Cu_1 arises noticeably nearer Cu_2 in *Melanitis.* The forewing veins are little inflated; any inflation is restricted to the base of Sc.

The hindwing cell is more or less rounded distad and is two-fifths to half the length of the wing measured to the end of M_3. The hind-wing vein Sc + R_1 is longer than 3A. Hindwing vein M_2 arises mid-way between M_1 and M_3, and veins M_3 and Cu_1 are well separated at their origins.

The pattern is similar to that of the Antirrhini with a shaded brown and orange upper surface and cryptic coloration on the under surface with a brown ground color and fine, dark striations.

Genera Included in the Melanitini

Cyllogenes Butler, 1868b: 6. Type-species: *Melanitis suradeva* Moore, by monotypy.

Gnophodes Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852: 363. Type-species: *Gnophodes parmeno* Westwood, designated by Butler, 1868a: 194.

Hipio Hübner, [1819] (1816-1826): 56. Type-species: *Papilio constantia* Cramer, designated by Butler, 1867a: 279.

Melanitis Fabricius, 1807: 282. Type-species: *Papilio leda* Linné, designated by Butler, 1868a: 194.
    = *Cyllo* Boisduval, 1832: 140. Type-species: *Papilio leda* Linné, designated by Scudder, 1875a: 151.

Parantirrhoea Wood-Mason, 1880: 248. Type-species: *Parantirrhoea marshallii* Wood-Mason, by monotypy.

Genus MANATARIA Kirby, 1908
(Figures 41-47)

Manataria Kirby, 1908: 57. Type-species: *Tisiphone hercyna* Hübner, by monotypy.
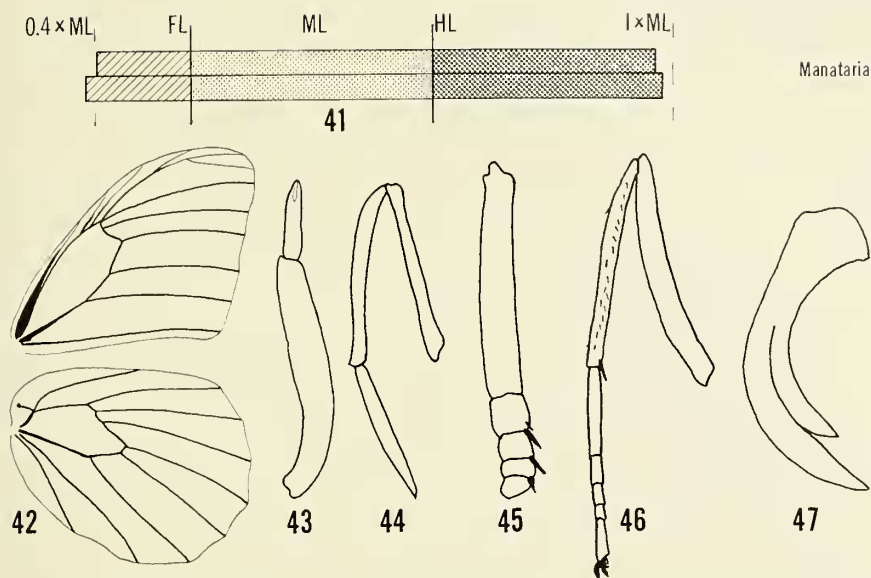
Figs. 41-47. *Manataria hercyna* (Hübner). 41. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling). The ML value is unity. The top bar represents the measurements obtained from the male, the bottom bar those from the female. 42. ♂ venation. 43. palpus. 44. ♂ foreleg. 45. ♀ foretarsus. 46. midleg. 47. bifid tarsal claw.

This South American genus has some morphological and pattern features which connect it to the *Neorina*-series of the Lethini. If this were its position, *Manataria* would be the only Neotropical lethine and not particularly closely related to the few Nearctic members of the tribe. The bifid tarsal claws, on the other hand, connect the present genus with the sympatric Antirrhini (although this is through the Paleotropical Melanitini), but in most other respects *Manataria* has little in common with the antirrhines. The pattern is quite typical of the *Neorina*-series, even to the basad displacement of the ocellus in hindwing space Rs-M_1 of the under surface. Were it not for the vast geographical isolation and the bifid tarsal claws I would place *Manataria* in the Lethini, perhaps in a monotypic series, but it seems more advisable to call attention to this aberrant genus here without assigning it to a tribe, pending further information. *Manataria* is characterized as follows:

The eyes are naked. The antennae are about half the length of the forewing costa; the antennal club is poorly developed and less than twice as thick as the shaft. The third segment of the palpus is just under one-third the length of the second. The hairs of the second palpal segment are not as long as the segment is wide.

The male foreleg is well developed with the tibia slightly longer than the femur and a monomerous, unspined tarsus. The female foreleg is also not significantly miniaturized with a pentamerous, un-clubbed tarsus which is spined on the second, third and fourth sub-segments. The midleg is slightly longer than the hindleg (Fig. 41). The midtibia is just less than twice as long as the proximal midtarsal subsegment, is slightly spinose dorsad, bears no spine at the dorsal, distal end and has well developed tibial spurs. The posttarsal claws are bifid. The relative lengths of the legs are shown in Fig. 41.

The forewing cell is produced at the origin of M_3 and about half as long as the forewing costa. The forewing radial veins arise in three branches from the cell, and Rs and M_1 are connate. Vein M_2 arises nearer M_1 than M_3, and Cu_1 arises slightly nearer M_3 than Cu_2. Forewing veins Sc and the cubital stem are slightly inflated; 2A is not.

The hindwing cell is produced at the origin of M_3 and is slightly more than two-fifths the length of the wing measured to the end of M_3. Veins $Sc + R_1$ and 3A are of about the same length, and M_3 and Cu_1 are separate, but approximate, at their origins. Vein M_2 arises much nearer M_1 than M_3.

The upper surface is dark brown with a transverse yellow spot-band on the forewing outside the cell. Below the pattern of the upper surface is repeated; in addition, there are pale scrawlings at the apex of the forewing and all over the hindwing and ocelli are developed in space M_1-M_2 of the forewing and in all spaces from Rs-M_1 to Cu_2-2A of the hindwing. The ocellus in hindwing space Rs-M_1 is displaced basad as in most of the Lethini.

Subfamily ELYMNIINAE Herrich-Schäffer, 1864

Eurytelidae Westwood, 1851, in Doubleday, Westwood and Hewitson, 1846-
    1852: 403 (in part).
Elymniina Herrich-Schäffer, 1864: 124.
= Enodiinae Clark, 1947: 149.
= Lethinae Clark, 1948: 77.

The Elymniinae are the now dominant primitive satyrid subfamily and apparently provided the source for the Satyrinae, Eritinae and probably the Ragadiinae — although the origin of the latter subfamily is still a problem. In some respects the elymniines may be connected to, and may have arisen from, the Melanitini (Biinae) through such genera as *Ptychandra* and *Samanta* (Lethini), as discussed under the melanitines.

Although not all Elymniinae show this characteristic and some that are not elymniines do, most satyrids with the hindwing veins M_3 and Cu_1 connate or closely approximate at their origins are probably referable to this subfamily. The form of the hindwing cell is also distinctive: it is usually greatly produced marginad at the origin of vein M_3, although this is not true of some Elymniini because of displacement of the venation by the androconial patch. The presence of androconial patches in specific locations is characteristic of the tribes. With the exception of a few lethine genera of the *Pararge*-series, the forewing cell is never more than half the length of the wing, in marked contrast with the preceding three subfamilies where the cell is seldom

TABLE 5

Some of the diagnostic characters of the tribes of the Elymniinae.

Character	Lethini	Zetherini	Elymniini	Mycalesini
Tibial spurs	Present	Present	Absent	Present
Eyes	Hairy, except in *Neorina*-series	Naked	Naked	Naked or hairy
Forewing vein 2A	Little, if at all, inflated	Not inflated	Not inflated	Subquadrate basal inflation, except two genera
Forewing median veins	M_2 arises nearer M_1 than M_3	M_2 arises much nearer M_1 than M_3	M_2 arises much nearer M_1 than M_3	M_2 arises much nearer M_1 than M_3
Forewing cell	Rounded, ca. 1/2 length of forewing	Slightly excavate, <1/2 length of forewing	Strongly excavate, <1/2 length of forewing	Strongly excavate, ca. 1/2 length of forewing

much less than three-fifths the length of the forewing costa.   The male foreleg is moderately well developed in all genera and is characteristically tapered to a rather sharp point.

The metropolis of the Elymniinae is the Paleotropical area, and three of the four tribes are found more or less exclusively there.   The other tribe, the Lethini, reaches its greatest development in the Indo-Malayan region but has representatives in Africa, the Palearctic and two genera in North America.

The tribes of the Elymniinae all more or less grade into one another.   They are the Lethini, Zetherini, Elymniini and Mycalesini. It is difficult to determine which of the tribes is primitive and which is derived, if any are, but the *Aeropetes*-series of the Lethini are definitely primitive, whatever the condition of the other members of the tribe; the other tribes have about equal status.   A key to the tribes of the Elymniinae is given below and an analysis of them in Table 5.

KEY TO THE TRIBES OF THE ELYMNIINAE

1. Tibial spurs absent (Fig. 96) .... Elymniini
    Tibial spurs present (Fig. 53, for example) 2
2. Forewing vein 2A inflated at base to a subquadrate thickening (Figs. 99,
        115, for example) .... most Mycalesini
    Forewing vein 2A, if thickened, not subquadrate at base 3
3. Eyes hairy; forewing cell frequently rounded distad (Fig. 49, for example)
        .... Lethini (except *Neorina*-series)
    Eyes naked; forewing cell frequently excavate (Fig. 90, for example) .. 4
4. Base of forewing vein Sc about three times the thickness of any other
        stalk (Fig. 106) .... Mycalesini (*Orsotriaena, Bletogona*)
    Bases of forewing veins little inflated, Sc seldom over twice the thickness
        of any other vein 5
5. Forewing vein M_2 arising much nearer M_1 than M_3 (m_1-m_2 one-fourth or
        less as long as m_2-m_3; Figs. 81, 86, 87) .... Zetherini
    Forewing arising nearer, but not much nearer, M_1 than M_3 ....
        .... Lethini (*Neorina* group)

Tribe LETHINI Clark, 1948
(Figures 48-80)

Enodiinae Clark, 1947: 149.
Lethinae Clark, 1948: 77.

"Lethinae" is used in preference to the older "Enodiinae" for a variety of reasons.   *Enodia* is generally considered at best a subgenus

of *Lethe,* but this is an invalid reason for the suppression of a family-group name, according to Art. 40 of the International Code of Zoological Nomenclature (1961). Part (a), however, of the same Article states, "If a family-group name, changed before 1961 because of such synonymy, has won general acceptance, it is to be maintained in the interests of stability." This is precisely applicable to the question at hand. Dos Passos (1964: 99) uses the collective name "Lethinae" in preference to the older "Enodiinae". To now replace Lethinae (or in this instance, "Lethini") with Enodiinae (Enodiini) would not serve the interests of stability of nomenclature. *Lethe* is further to be preferred, all other things being equal, inasmuch as this genus is recognized throughout much of the world; *Enodia,* where it is even recognized today, is known only in the eastern part of North America.

The Lethini may be the focal point of much of the evolution of the higher categories of the Satyridae. As mentioned earlier in the discussion of the Melanitini, there are some vaguely but intriguingly indicated connections between that group and the lethines through such lethine genera as *Ptychandra* and *Samanta.* The venation of the former genus, while highly modified by androconial displacement of the forewing veins, is suggestive of the pattern in the melanitines (Fig. 57). *Samanta,* while a perfectly typical lethine from almost all other aspects, does show the bifid tarsal claws which characterize the Melanitini and the Neotropical aberrant genus *Manataria.* Within the Elymniinae, too, some interesting gradations may be seen. The line separating the Zetherini from the Lethini is a thin one, based chiefly on the relative positions of some veins and naked *versus* hairy eyes, respectively. The zetherines, in turn, have many characteristics in common with the Elymniini, as will be shown below. The genus *Mandarinia* is a puzzle: the distribution of androconia suggest that it is a mycalesine, but the lack of inflation of the forewing vein 2A and the distally rounded forewing cell are lethine characteristics: this genus is provisionally placed in the Lethini (Fig. 73). The African members of the *Aeropetes*-series show yet another relationship. If one considers these butterflies and members of the satyrine tribe Dirini together, one can almost obtain a graded series from perfectly good Lethini to typical Satyrinae. This is probably convergence, as will be shown later.

The Lethini are generally characterized by the hairy eyes which separate them from the Elymniini and the zetherines, the presence of tibial spurs (a characteristic of the Elymniini is the lack of tibial spurs) and by the more or less rounded forewing cell, never excavate as in the elymniines and most mycalesines. Most Lethini show a characteristic basad displacement (diastoma) of the hindwing ocellus in space M_1-M_2. There are a number of generic series, however, so it is difficult to distinguish all lethines by a single set of criteria.

The *Aeropetes*-series, consisting of two genera, is confined to South Africa and characterized by the large size, extremely primitive pattern (Schwanwitsch, 1924), hairy eyes, connate hindwing veins M_2 and Cu_1, extremely spiny midtibia and lack of androconial patches (Figs. 67-72).

The *Lethe*-series, *sensu stricto*, has twenty-five nomenclatorially, though not necessarily biologically, valid genera, twenty-two of which are Indo-Australian or sub-Palearctic, one East African and two North American. These insects are medium to large-sized, have a rather primitive pattern on the under surface, though not necessarily on the upper, hairy eyes, connate to separate hindwing veins M_3 and Cu_1, dorsally smooth to only slightly spiny midtibia and frequently with androconial patches in the usual positions (Figs. 49-59, 66).

The *Pararge*-series has nine Palearctic genera which differ from the *Lethe*-series chiefly in the length of the forewing cell: in all other groups the cell is about half the length of the wing, whereas in *Pararge* and its allies it is about three-fifths as long (Figs. 60-65).

The *Mandarinia*-series is monotypic, and is characterized by its *Mycalesis*-like androconial area and is found exclusively in China (Figs. 73-76).

The *Neorina*-series is composed of four Indo-Australian genera. These butterflies are characterized by their large size, highly modified pattern, naked eyes, spiny midtibia and lack of androconia (Figs. 77-80).

The Lethini are characterized as follows:

The eyes are hairy in all members except those of the *Neorina*-series, which have naked eyes. The antennae are generally from two-fifths to nearly half as long as the forewing costa, but the antennae are slightly longer than half the costa in such genera as *Hermias*, *Tansima* and *Pararge*. The antennal club is moderately well devel-
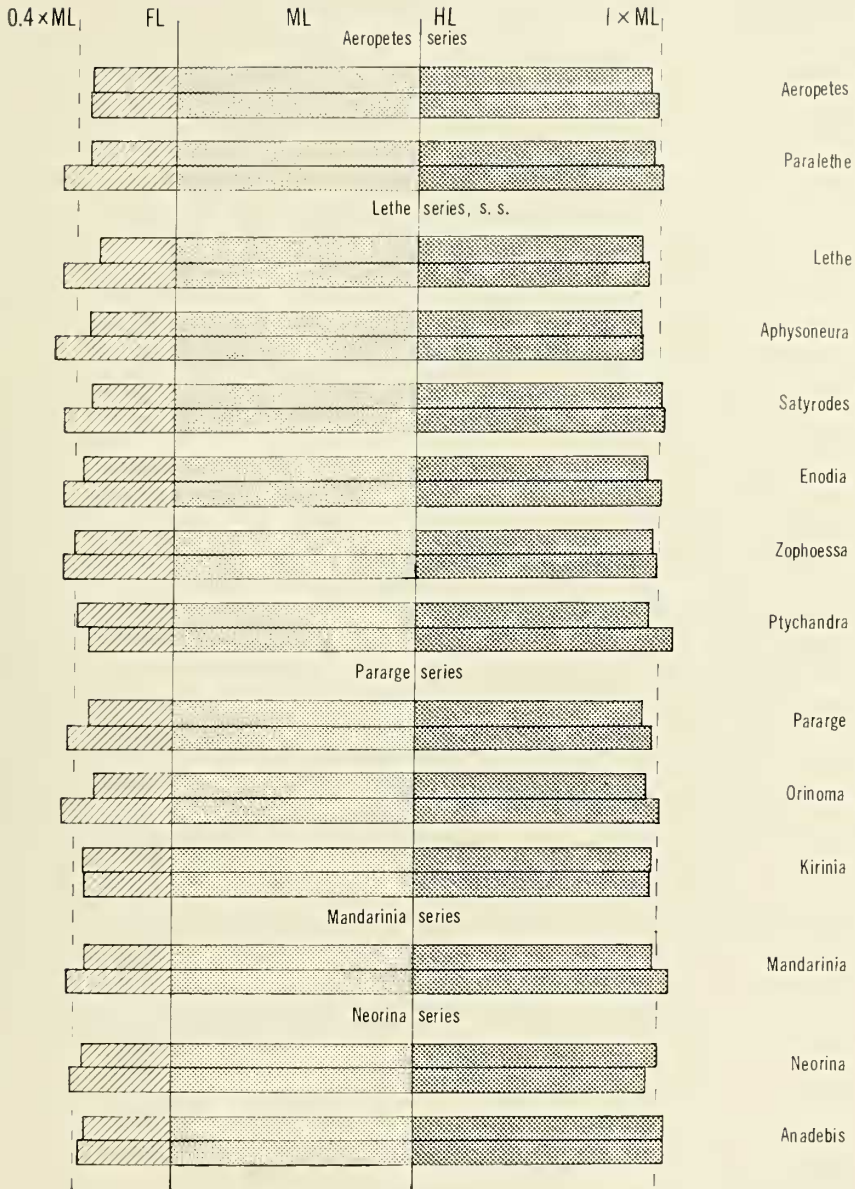
Fig. 48. Elymniinae: Lethini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

oped, occupying the distal quarter of the antenna and inflated two to three times the thickness of the shaft. The relative lengths of the second and third segments of the palpus are highly variable within the tribe: the third segment is less than one-sixth the length of the second in *Crebeta* and between one-third and one-half in *Hermias*; in most genera the third palpal segment is one-fourth to one-fifth the length of the second. The length of the hairs of the second segment of the palpus is also variable: the hairs are shorter than the segment is wide in *Hermias,* but four times as long as the segment is wide in such genera as *Magula* and *Lopinga*; in most genera the hairs are about three times as long as the second segment is wide.

The development of the male foreleg is also variable, although the leg itself is relatively unminiaturized. There is a great variation in the relative length of the forefemur and tibia, and the tarsus has one to three subsegments and is usually unspined, although there are many tarsal spines in such genera as *Ethope* and *Paralethe*. The female foreleg is likewise well developed and slightly clubbed at the end of the tarsus. The tarsus is always pentamerous with spines on at least the second, third and fourth subsegments (also on the first subsegment in such genera as *Lethe* and *Ptychandra*). The mid- and hindlegs are of about the same length. The midtibia is always less than twice the length of the first midtarsal subsegment. In the South African *Aeropetes* and *Paralethe* the midtibia is extremely spinose dorsad (Fig. 71), but the midtibia is smooth in other genera, such as *Lethe* and *Satyrodes* (Fig. 53). The tibial spurs are always present and well developed, but there is no spine at the dorsal, distal end of the midtibia. The relative lengths of the legs are shown in Fig. 48.

The following cell is square-cut or rounded distad, never excavate as in other elymniine tribes, and about half as long as the forewing costa (Fig. 49, for example)—but this characteristic is by no means universal. In *Ptychandra* the cell is only a third the length of the wing (Fig. 57), and in most members of the *Pararge*-series the cell is about three-fifths the length of the costa (Figs. 60, 64, 65). The forewing radial veins always arise in three branches from the cell, and veins Rs and M_1 are usually well separated at their origins, although they may arise approximate to one another. Forewing vein M_2 arises nearer, though not much nearer, M_1 than M_3; and Cu_1 arises midway
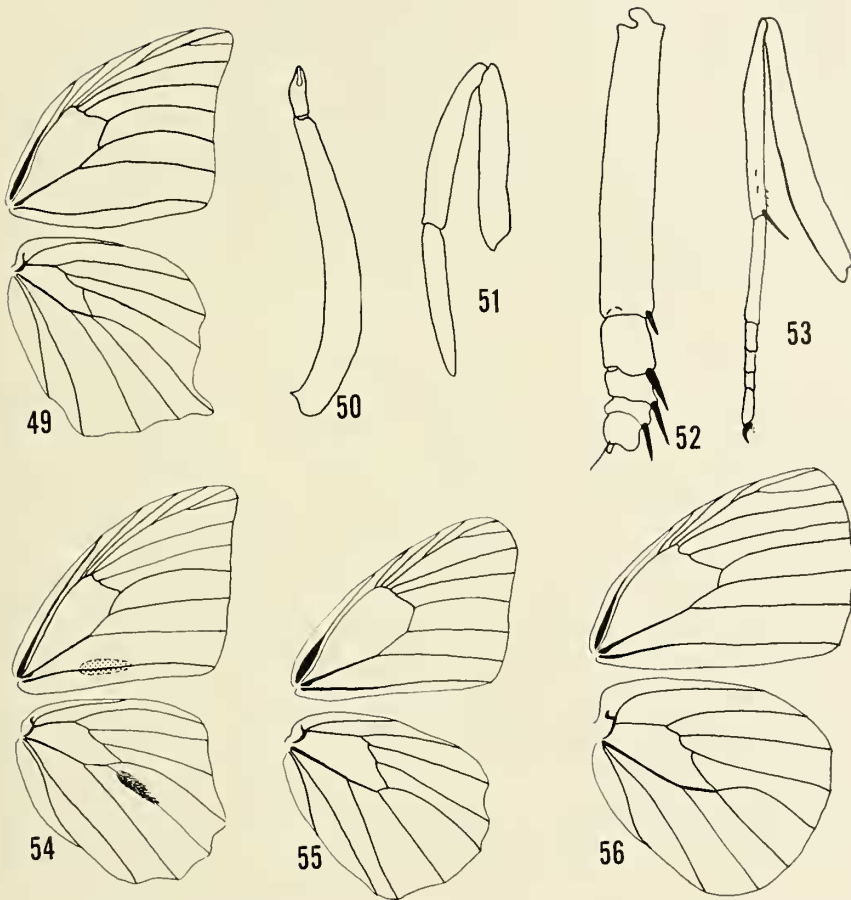
Figs. 49-56. Elymniinae: Lethini. 49. *Lethe europa* (Fabricius), ♂ vena-
tion. 50. *L. europa*, palpus. 51. *L. europa*, ♂ foreleg. 52. *L. europa*, ♀ fore-
tarsus. 53. *L. europa*, midleg. 54. *Rangbia scanda* (Moore), ♂ venation.
55. *Rhaphicera satricus* (Westwood and Hewitson), ♂ venation. 56. *Tansima
satyrina* (Butler), ♂ venation.

between M_3 and Cu_2 in most genera, but Cu_1 arises nearer Cu_2 in
several genera (*e.g., Lethe*, Fig. 49, *Ptychandra*, Fig. 57, and *Pararge*,
Fig. 60). Forewing vein Sc is often somewhat inflated, the cubital
stem seldom inflated, although it is much inflated in *Ptychandra*, and
2A is never much swollen.

The hindwing cell is produced at the origin of vein M_3 and is

two-fifths to three-fifths the length of the wing measured to the end of
M_3. Hindwing vein $Sc + R_1$ is of equal length or shorter than 3A.
Veins M_3 and Cu_1 are usually connate, but they are well separated
in such aberrant genera as *Mandarinia, Ptychandra* and *Rhaphicera*.
Vein M_2 usually arises nearer M_1 than M_3, though not much nearer.
In *Aeropetes* M_2 arises midway between M_1 and M_3, slightly nearer
M_3 in the *Pararge*-series and much nearer M_3 in *Mandarinia*.

The pattern is highly variable, the main unifying feature being the
diastoma of the hindwing ocelli in space M_1-M_2 which was mentioned
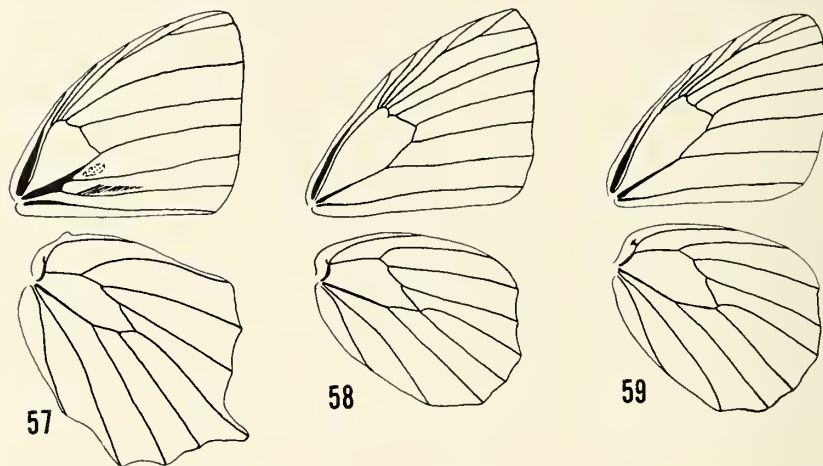
Figs. 57-59.   Elymniinae: Lethini.   57. *Ptychandra lorquinii* Felder and
Felder, ♂ venation.   58. *Enodia portlandia* (Fabricius), ♂ venation.   59. *Saty-
rodes eurydice* (Linné), ♂ venation.

earlier.   This characteristic is by no means universal, though, and is
lacking in many genera, either because of the loss of many ocelli or
extensive realignment of all the hindwing spots.   There are several
sites of androconial generation in the Lethini.   Forewing patches are
uncommon and restricted to the area between the origin of the cubitus
and the inner margin.   These forewing patches are rarely hair tufts
(*Ptychandra*, Fig. 57) and are more frequently small patches of mealy
scales under the origin of Cu_1.   The hindwing androconial patches
are much more common and usually lie just outside the cell between
M_3 and Cu_2, although *Mandarinia* has a *Mycalesis*-like hair tuft along
vein Rs (Fig. 73).   Hindwing hair tufts are commoner than mealy
patches, but both are present throughout the tribe.

Genera Included in the Lethini

Aeropetes-series

Aeropetes Billberg, 1820: 79.   Type-species: *Papilio tulbaghia* Linné, designated by Hemming, 1943: 23.
>   = *Meneris* Westwood, 1850, *in* Doubleday, Westwood and Hewitson, 1846-1852: 296.   Type-species: *Papilio tulbaghia* Linné, by monotypy.

Paralethe van Son, 1955: 51.   Type-species: *Satyrus dendrophilus* Trimen, by original designation.

Lethe-series, sensu stricto

Aphysoneura Karsch, 1894: 190.   Type-species: *Aphysoneura pigmentaria* Karsch, by original designation.
>   = *Rhaphiceropsis* Sharpe, 1894: 336.   Type-species: *Rhaphiceropsis pringlei* Sharpe (= *Aphysoneura pigmentaria* Karsch), by original designation.

Archondesa Moore, 1892 (1890-1893): 270.   Type-species: *Lethe lanaris* Butler, by original designation.

Charma Doherty, 1886: 117.   Type-species: *Zophoessa baladeva* Moore, by original designation.   Proposed as a subgenus of *Lethe* Hübner.
>   = *Putlia* Moore, 1892 (1890-1893): 287.   Type-species: *Zophoessa baladeva* Moore, by original designation.   Proposed to replace *Charma* Doherty, wrongly believed to be preoccupied.

Choranesa Moore, 1892 (1890-1893): 270.   Type-species: *Lethe trimacula* Leech, by original designation.

Debis Doubleday and Hewitson, 1849, *in* Doubleday, Westwood and Hewitson, 1846-1852: pl. 61.   Type-species: *Debis samio* Doubleday and Hewitson, by monotypy.

Dionana Moore, 1892 (1890-1893): 271.   Type-species: *Lethe margaretae* Elwes, by original designation.

Enodia Hübner, [1819] (1816-1826): 61.   Type-species: *Enodia andromacha* Hübner (= *Papilio portlandia* Fabricius), designated by Scudder, 1872: 26.

Hanipha Moore, 1880 (1880-1881): 18.   Type-species: *Lethe sihala* Moore (= *Lethe dynsate* Hewitson), by original designation.   This name is commonly misspelled "*Hanifa*".

Harima Moore, 1892 (1890-1893): 299.   Type-species: *Neope callipteris* Butler, by original designation.

Hermias Fruhstorfer, 1912 (1912-1915): 324.   Type-species: *Satyrus verma* Kollar, by monotypy.   Proposed as a "subgenus or species-group" of *Lethe* Hübner.

Kerrata Moore, 1892 (1890-1893): 285.   Type-species: *Lethe tristigmata* Elwes, by original designation.

Kirrodesa Moore, 1892 (1890-1893): 237.   Type-species: *Debis sicelis* Hew-
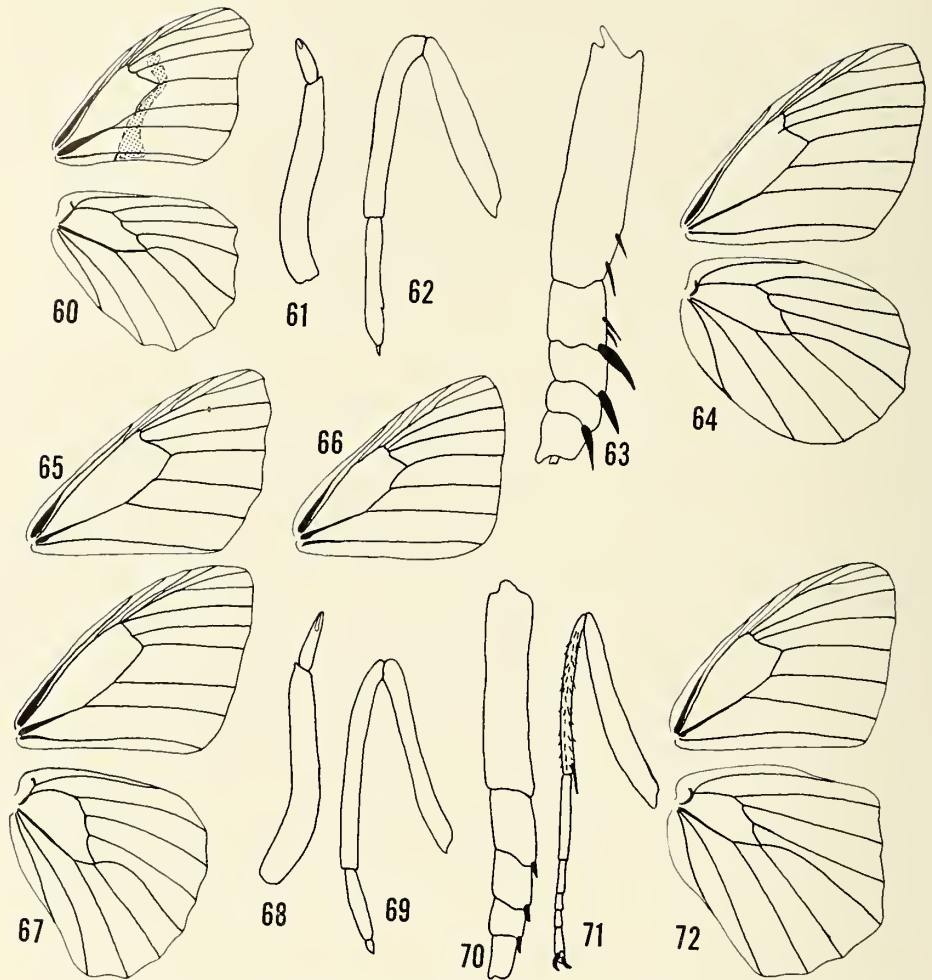
Figs. 60-72. Elymniinae: Lethini. 60. *Pararge aegeria* (Linné), ♂ vena-
tion. 61. *P. aegeria*, palpus. 62. *P. aegeria,* ♂ foreleg. 63. *P. aegeria*, ♀
foretarsus. 64. *Crebeta deidamia* (Eversmann), ♂ venation. 65. *Lopinga
dumetorum* (Oberthür), venation of ♂ forewing. 66. *Aphysoneura pigmentaria*
Karsch. venation of ♂ forewing. 67. *Aeropetes tulbaghia* (Linné), ♂ venation.
68. *A. tulbaghia*, palpus. 69. *A. tulbaghia*, ♂ foreleg. 70. *A. tulbaghia*, ♀
foretarsus. 71. *A. tulbaghia*, midleg. 72. *Paralethe dendrophilus* (Trimen),
♂ venation.

itson, by original designation.

Lethe Hübner, [1819] (1816-1826): 56. Type-species: *Papilio europa* Fabri-
cius, by monotypy.
= *Tanaoptera* Billberg, 1820: 79. Type-species: *Papilio europa* Fab-

ricius, designated by Hemming, 1933: 199.

Magula Fruhstorfer, 1912 (1912-1915): 313. Type-species: *Zophoessa jala-urida* deNicéville, designated by Hemming, 1935: 1. Preoccupied by *Magula* Scudder (Megerle MS.), 1882, but no replacement name has been proposed.

Nemetis Moore, 1892 (1890-1893): 237. Type-species: *Papilio minerva* Fabricius, by original designation.

Neope Butler, 1867d: 166. Type-species: *Lasiommata* (?) *bhadra* Moore, designated by Butler, 1868b: 112.

    = *Enope* Moore, 1857: 228. Type-species: *Lasiommata* (?) *bhadra* Moore, designated by Moore, 1892 (1890-1893): 299. Preoccupied by *Enope* Walker, 1854.

    = *Blanaida* Kirby, 1877: 699. Type-species: *Lasiommata* (?) *bhadra* Moore, by original designation. Proposed to replace *Enope* Moore.

Ninguta Moore, 1892 (1890-1893): 310. Type-species: *Pronophila schrenkii* Ménétriés, by original designation.

    = *Aranda* Fruhstorfer, 1909: 134. Type-species: *Pronophila schrenkii* Ménétriés, by original designation.

Patala Moore, 1892 (1890-1893): 305. Type-species: *Zophoessa yama* Moore, by original designation.

Placilla Moore, 1892 (1890-1893): 253. Type-species: *Lethe christophi* Leech, by original designation.

Ptychandra Felder and Felder, 1861: 304. Type-species: *Ptychandra lorquinii* Felder and Felder, by monotypy.

Rangbia Moore, 1892 (1890-1893): 232. Type-species: *Debis scanda* Moore, by original designation.

Samanta Moore, 1880: 166. Type-species: *Mycalesis malsara* Moore, by original designation.

Satyrodes Scudder, 1875b: 242. Type-species: *Papilio eurydice* Linné, by original designation.

    = *Argus* Scopoli, 1777: 432. Type-species: *Papilio eurydice* Linné, designated by Scudder, 1872: 27. Preoccupied by *Argus* Bohadsch, 1761.

Sinchula Moore, 1892 (1890-1893): 275. Type-species: *Debis sidonis* Hewitson, by original designation.

Tansima Moore, 1881: 305. Type-species: *Lethe satyrina* Butler, by monotypy.

Zophoessa Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852: 362. Type-species: *Zophoessa sura* Westwood, by monotypy.

Pararge-series

Chonala Moore, 1893 (1890-1893): 14. Type-species: *Debis* (*Tansima*) *masoni* Elwes, by original designation.

Crebeta Moore, 1893 (1890-1893): 11. Type-species: *Pararge deidamia* Eversmann, by original designation.

Kirinia Moore, 1893 (1890-1893): 14. Type-species: *Lasiommata epimenides* Ménétriés, by original designation.

Lasiommata Westwood, 1841: 65. Type-species: *Papilio megera* Linné, designated by Scudder, 1875a: 202.

     = *Amecera* Butler, 1867d: 162. Type-species: *Papilio megera* Linné, designated by Butler, 1868b: 123.

Lopinga Moore, 1893 (1890-1893): 11. Type-species: *Pararge dumetorum* Oberthür, by original designation.

Orinoma Gray, 1846: 14. Type-species: *Satyrus* (?) *damaris* Doubleday (*nec.* Gray), by monotypy.

Pararge Hübner, [1819] (1816-1826): 59. Type-species: *Papilio aegeria* Linné, designated by Butler, 1868a: 195. This name has been frequently misspelled as "*Pararga*" or "*Parage*" in the literature.

Rhaphicera Butler, 1867d: 164. Type-species: *Lasiommata satricus* Westwood and Hewitson, designated by Butler, 1868b: 158.

Tatinga Moore, 1893 (1890-1893): 5. Type-species: *Satyrus thibetanus* Oberthür, by original designation.

Mandarinia-series

Mandarinia Leech, 1892: 9. Type-species: *Mycalesis regalis* Leech, by original designation.

Neorina-series

Ethope Moore, 1865: 770. Type-species: *Mycalesis* (?) *himachala* Moore, by monotypy.

     = *Theope* Moore, 1857: 234. Type-species: *Mycalesis* (?) *himachala* Moore, by original designation. Preoccupied by *Theope* Doubleday and Hewitson, 1847.

     = *Anadebis* Butler, 1867c: 50. Type-species: *Mycalesis* (?) *himachala* Moore, by monotypy.

Euploeamina Holland, 1887: 113. Type-species: *Zethera diademoides* Moore, by original designation.

Hermianax Fruhstorfer, 1912 (1912-1915): 326. Type-species: *Neorina latipicta* Fruhstorfer (= *Neorina lowi* Doubleday and Hewitson), by original designation. Proposed as a subgenus of *Neorina* Westwood.

Neorina Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852: 369. Type-species: *Neorina hilda* Westwood, by original designation.

Figs. 73-87. Elymniinae: Lethini (Figs. 73-80) and Zetherini (Figs. 81-87). 73. *Mandarinia regalis* (Leech), ♂ venation. 74. *M. regalis*, palpus. 75. *M. regalis*, ♀ foretarsus. 76. *M. regalis*, midleg. 77. *Neorina hilda* Westwood, ♂ venation. 78. *N. hilda*, ♂ foreleg. 79. *N. hilda*, ♀ foretarsus. 80.
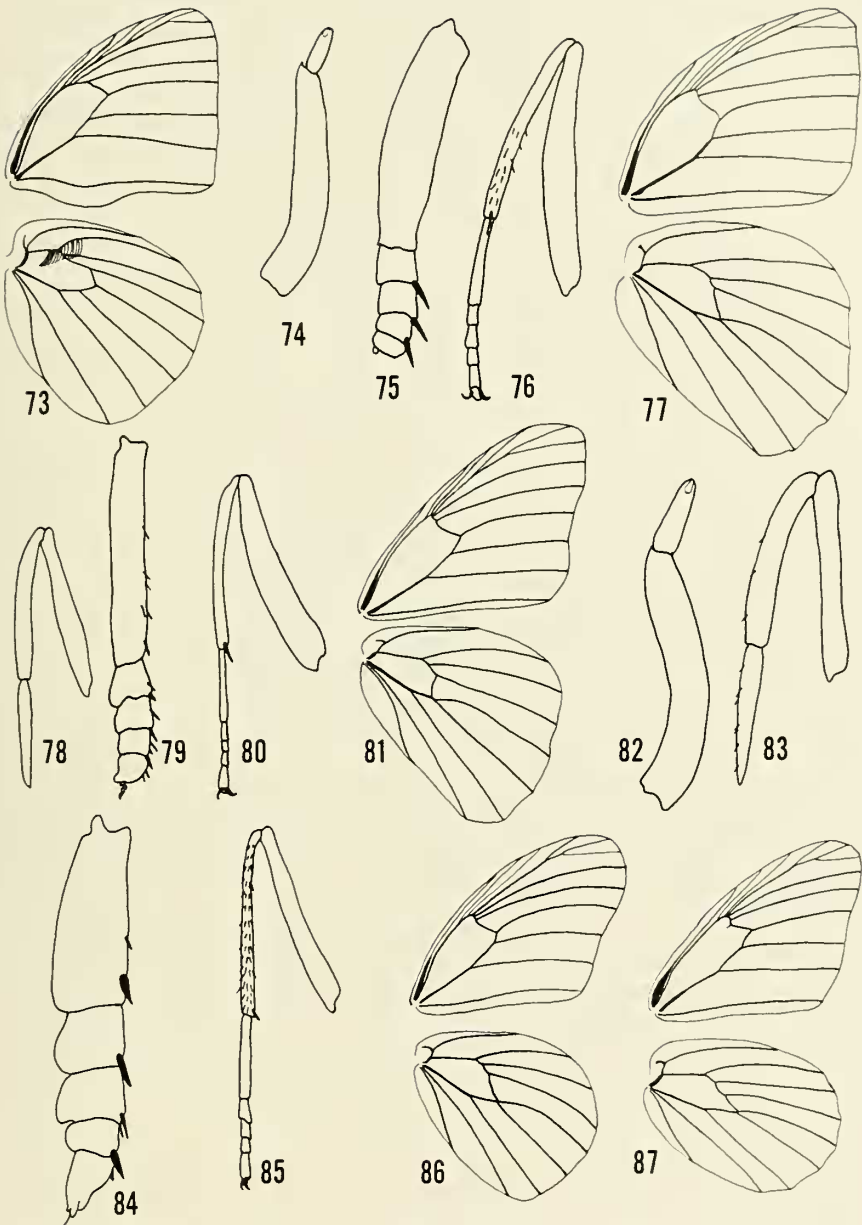
N. hilda, midleg.   81. *Zethera pimplea* (Erichson), ♂ venation.   82. *Z. pim-plea*, palpus.   83. *Z. pimplea*, ♂ foreleg.   84. *Z. pimplea*, ♀ foretarsus.   85. *Z. pimplea*, midleg.   86. *Amechania incerta* Hewitson, ♂ venation.   87. *Callarge sagitta* (Leech), ♂ venation.

Tribe ZETHERINI, new tribe

(Figures 81-88)

The zetherines have been considered part of the Elymniini by such authors as Gaede (1931), and while these two tribes share such features as close forewing veins M_2 and Cu_1, they are abundantly distinct. Perhaps the closest relatives of the zetherines are certain of the more primitive lethines such as *Aeropetes,* but the differences discussed below also serve to separate these two tribes. The pattern of the zetherines is highly aberrant: several species are white with brown interveinal markings and either no ocelli or poorly developed ones, whereas *Zethera pimplea* (Erichson) looks like the Nearctic
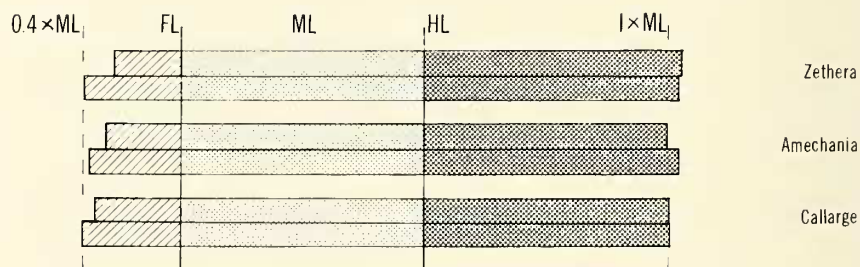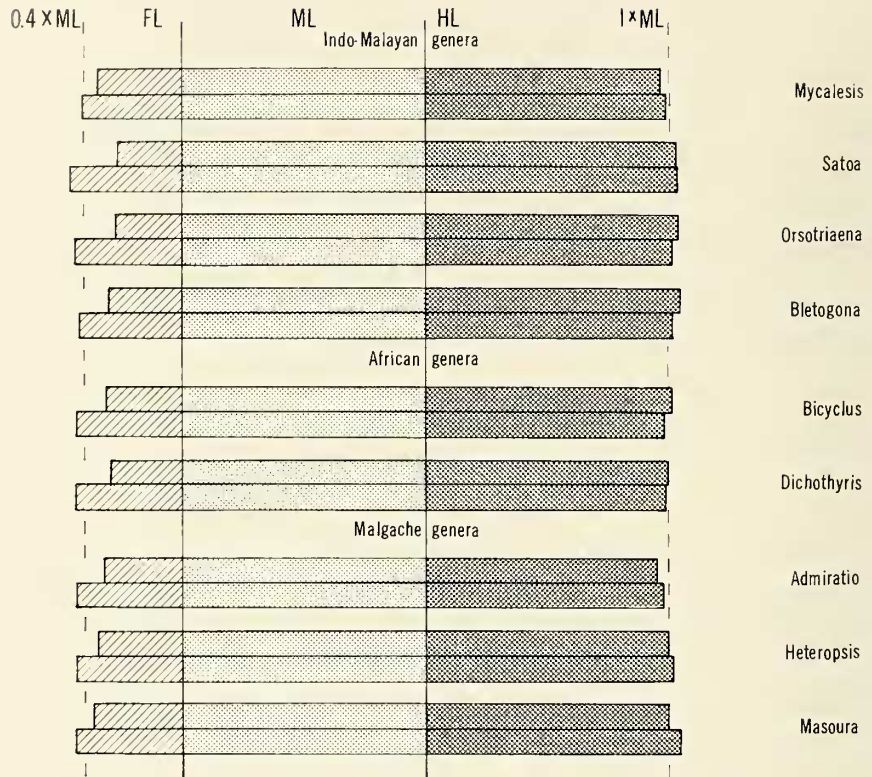

Fig. 88. Elymniinae: Zetherini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of the genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

Limenitis weidemeyeri (Edwards) (Nymphalidae: Limenitinae), a black species with a wide white central band crossing both wings.

The absence of inflation of the forewing veins serves to distinguish this tribe from the Mycalesini, while the spiny midtibia and the well developed tibial spurs separate the Zetherini from the Elymniini. Most Lethini, with the exception of the *Neorina*-series, have hairy eyes, whereas all zetherines have naked eyes. The relative position of the forewing veins M_3, Cu_1 and Cu_2 serve to distinguish members of this tribe from the *Neorina*-series of the Lethini. All the members of the Zetherini are Indo-Australian. The zetherines are characterized as follows:

The eyes are naked. The antennae are just over two-fifths the

length of the forewing costa.   The antennal club is weakly developed and gently tapered, never more than twice the thickness of the shaft. The relative lengths of the second and third segments of the palpus are variable: in *Callarge* the third segment is about one-seventh as long as the second, whereas in *Zethera* it is one-third as long.   The hairs of the second segment of the palpus are always shorter than the segment is wide.

The male foreleg is well developed with the femur longer than the tibia and a mono- to trimerous tarsus which may or may not bear spines.   The female foreleg is also well developed with a pentamerous, slightly clubbed tarsus bearing spines on the first four subsegments. The hindlegs are equal to or slightly longer than the midlegs (Fig. 88).   The mid-tibia is long——twice to two and a half times as long as the first midtarsal subsegment—and the midtibia is spiny dorsad, bearing moderately well developed tibial spurs, but no spine at the dorsal, distal end.

The forewing cell is slightly excavate and two-fifths to half as long as the forewing costa.   The forewing radial veins arise from the cell in three branches, and veins Rs and M_1 are approximate, but not connate, at their origins.   Vein M_2 arises much nearer M_1 than M_3, and Cu_1 arises much nearer M_3 than Cu_2.   None of the forewing veins are much inflated basally.

The hindwing cell is strongly produced at the origin of M_3 and is one-third to half the length of the wing measured to the end of M_3.   Hindwing vein $Sc + R_1$ is longer than 3A.   Veins M_3 and Cu_1 are connate, or nearly so, and M_2 arises nearer (or in some cases, much nearer) M_1 than M_3.

The pattern of all the species is aberrant.   *Callarge* is cream-colored with dark veins.   *Amechania* is whitish with dark veins, some dark interveinal markings and a few ocelli.   *Zethera* is blackish-brown with broad discal white bands on all wings.   There are no defined androconial patches on any zetherine.

Genera Included in the Zetherini

Amechania Hewitson, 1861 (1856-1876): 87.   Type-species: *Amechania incerta* Hewitson, by monotypy.

Callarge Leech, 1892: 57.   Type-species: *Zethera sagitta* Leech, by original designation.

Zethera C. Felder, 1861: 26. Type-species: *Cynthia pimplea* Erichson, by monotypy.

Tribe ELYMNIINI Herrich-Schäffer, 1864

(Figures 89-97)

Eurytelidae Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852: 403 (in part).
Elymniina Herrich-Schäffer, 1864: 124.

The Elymniini are a homogeneous group and show some affinities within the subfamily. There is little to connect the elymniines with the Lethini directly, but the positions of certain of the veins show a definite relationship between these butterflies and the zetherines, which in turn do relate to the Lethini. The deeply excavate forewing cell of these insects is approached in the Mycalesini, and many of the latter groups have androconial patches placed very like those which characterize the Elymniini.
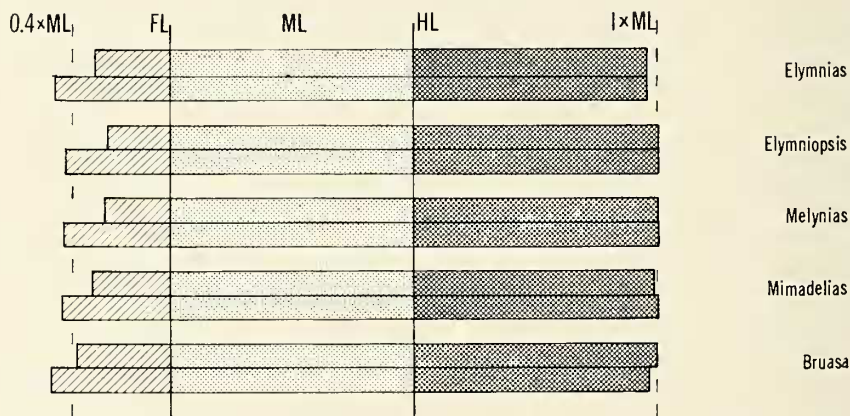
Fig. 89. Elymniinae: Elymniini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

This tribe may be distinguished from all others within the subfamily by the lack of tibial spurs in all species. Many of the genera also have extremely short cells on both wings, but there are a few exceptions.

All elymniines are Paleotropical, most being found in the Indo-Australian region, but a couple of species range as far west as West Africa. The Elymniini are characterized in the following paragraphs.

The eyes are naked. The antennae are about two-fifths as long are the forewing costa, although they may be as much as 0.46 times as long as the costa. The antennal club is very gentle and seldom more than twice the width of the shaft, except in the genus *Melynias* where it is over twice the thickness of the shaft. The third segment of the palpus is from one-fifth (*Melynias*) to one-third (*Dyctis*) the length of the second segment. The hairs of the second palpal segment are about as long as the segment is wide.

The male foreleg is well developed with the femur longer than the tibia and with a monomerous, unspined tarsus. The female foreleg is also well developed with a pentamerous, unclubbed tarsus bearing a double set of spines on the third and fourth subsegments (also a double set on the second subsegment in *Elymniopsis*). The mid- and hindlegs are of about the same length (Fig. 89). The midtibia is generally less than twice the length of the first midtarsal subsegment and is smooth dorsad, without tibial spurs or a spine at the dorsal, distal end.

The forewing cell is usually deeply excavate (Figs. 90-92) and is always less than half the length of the forewing costa. Frequently the cell is less than a third as long as the costa. The forewing radial veins arise in three branches from the cell, and Rs and M_1 are well separated at their origins. Vein M_2 arises much nearer M_1 than M_3, and Cu_1 is almost connate with M_3, never near Cu_2. Forewing vein Sc is usually inflated basad; the other stems are not.

The hindwing cell is more or less square-cut because of the displacement marginad of M_1 and is from one-third to almost half as long as the wing measured to the end of M_3. Hindwing vein $Sc + R_1$ is always much shorter than 3A. Veins M_3 and Cu_1 are always connate, or nearly so, and M_2 arises much nearer M_1 than M_3.

The pattern is quite variable and has been considered a mimetic one. Many of the species resemble various Danaidae, particularly of the genus *Euploea*. For a description of most of the species see Moore, 1893 (1890-1893).
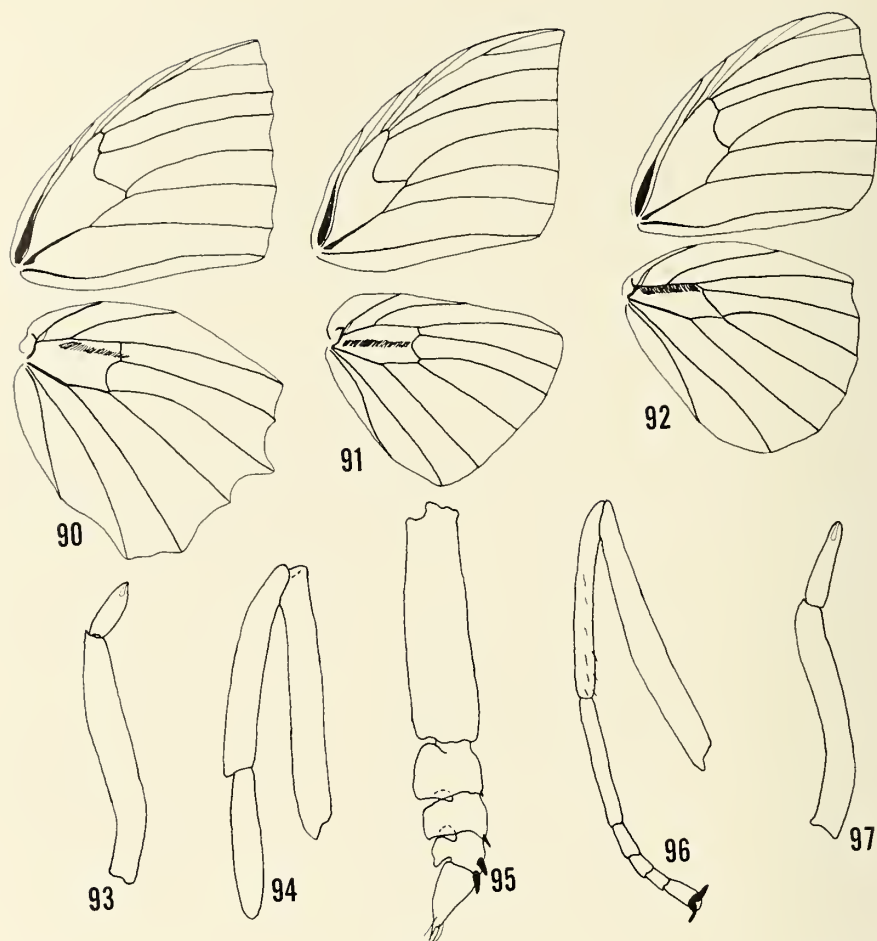
Figs. 90-97. Elymniinae: Elymniini. 90. *Elymnias hypermnestra* (Linné), ♂ venation. 91. *Bruasa penanga* (Westwood and Hewitson), ♂ venation. 92. *Dyctis agondas* Boisduval, ♂ venation. 93. *E. hypermnestra*, palpus. 94. *E. hypermnestra*, ♂ foreleg. 95. *E. hypermnestra*, ♀ foretarsus. 96. *E. hypermnestra*, midleg. 97. *Elymniopsis lise* Hemming, palpus.

Genera Included in the Elymniini

Agrusia Moore, 1893 (1890-1893): 144. Type-species: *Melanitis esaca* Westwood and Hewitson, by original designation.

Bruasa Moore, 1893 (1890-1893): 144. Type-species: *Melanitis penanga* Westwood and Hewitson, by original designation.

Didonis Hübner, [1819] (1816-1826): 17. Type-species: *Papilio vitellia* Cramer, designated by Scudder, 1875a: 156.

Dyctis Boisduval, 1832: 138. Type-species: *Dyctis agondas* Boisduval, by monotypy.

Elymnias Hübner, 1818 (1818-1825): 12. Type-species: *Elymnias jynx* Hübner (= *Papilio hypermnestra* Linné), designated by Hemming, 1943: 24. Scudder (1875a: 162) designated *Papilio lais* Fabricius as type, based on *Elymnias* Hübner, [1819] (1816-1826): 37. This designation was invalidated when the appropriate sections of the "Zuträge" were found to be older than those of the "Verzeichniss".

Elymniopsis Fruhstorfer, 1907: 171, 173-174. Type-species: *Papilio phegea* Fabricius (= *Elymniopsis lise* Hemming), designated by Hemming, 1943: 24.

Melynias Moore, 1893 (1890-1893): 144. Type-species: *Papilio lais* Cramer (= *Papilio nesaea* Linné), by original designation.

Mimadelias Moore, 1893 (1890-1893): 144. Type-species: *Elymnias vasudeva* Moore, by original designation.

Tribe MYCALESINI, new tribe

(Figures 98-119)

The mycalesines show rather close relationships to both the Lethini and the Elymniini. Such mycalesine genera as *Orsotriaena* and *Bletogona* lack the characteristic inflation of the veins, but do have the excavate forewing cell and the distinctive androconial patches, whereas the lethine *Mandarinia regalis* (Leech) has the androconial patch but lacks the inflation of forewing vein 2A or the excavate forewing cell. The excavate forewing cell and the presence in some genera of a hair tuft on the upper surface of the hindwing at the anterior margin of the cell strongly suggests a relationship between the Mycalesini and the Elymniini.

The characteristic subquadrate shape of the basal inflation of forewing vein 2A serves to distinguish the vast majority of all mycalesines. In the Hypocystini (Satyrinae) this inflation of 2A is suggested, but in that tribe the inflation is in the form of a rounded knot, rather than a subquadrate thickening, as in the present tribe.

The Mycalesini are general throughout the Old World tropics and form a homogeneous group. There is some regional correlation of genera in the tribe, and for that reason they are arranged geographically here. It is interesting to note that although hairy or naked eyes do not characterize the tribe, all mainland African Mycalesini have naked eyes, all those from Madagascar have hairy eyes and both states are found in the Indo-Australian genera. This
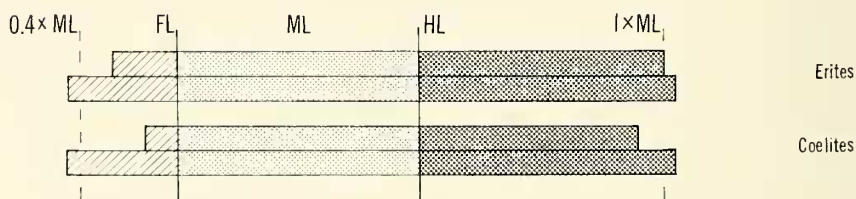
Fig. 98.   Elymniinae: Mycalesini.   Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hind legs (HL, heavy stippling) of selected genera.   In all instances the ML value is unity.   The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

situation will be discussed further in the section on "Evolution and Zoogeography."   The Mycalesini are characterized as follows:

The eyes are naked or hairy: the Indo-Australian species show both conditions, those from mainland Africa all have naked eyes and those from Madagascar have hairy eyes.   The antennae are from two-fifths to half the length of the forewing costa.   The antennal club is moderately well developed, occupying the distal one-third to one-fifth of the antenna and thickened from less than twice (*Orsotriaena*) to more than three times (such genera as *Dalapa* and *Martanda*) the thickness of the shaft.   The third segment of the palpus is usually one-third to one-fifth the length of the second segment, but the third

segment is more than half as long as the second in *Dalapa*. The hairs of the second palpal segment are generally from as long as the segment is wide to twice the width of the segment.

The male foreleg is well developed with the femur longer than the tibia and one or (rarely) two unspined or weakly spined tarsal subsegments. The female foreleg is moderately well developed with a pentamerous, lightly clubbed (less so in genera from Madagascar, Fig. 118) tarsus bearing spines on at least the fourth subsegment, often also on the second and third and occasionally on the first (such genera as *Martanda*). The mid- and hindlegs are not significantly unequal. The midtibia is less than twice as long as the first midtarsal subsegment. The midtibia is usually unspined dorsad, although it is weakly spined in *Orsotriaena* (Fig. 108), etc.; tibial spurs are always present and well developed and there is no spine at the dorsal distal end of the midtibia.

The forewing cell is excavate and varies little from half the length of the forewing costa. The forewing radial veins arise in three branches from the cell, and veins Rs and M_1 arise separate, but approximate, from the cell. Vein M_2 arises much nearer M_1 than M_3, and Cu_1 arises nearer M_3 than Cu_2. The pattern of basal inflation of the forewing veins is characteristic, except in *Orsotriaena* (Fig. 106) and *Bletogona*: veins Sc and the cubital stem are inflated normally, but markedly, and 2A is inflated near its base as a sub-quadrate knot.

The hindwing cell is produced at M_3 and is one-third to half as long as the wing measured to the end of M_3. Hindwing vein $Sc + R_1$ is as long as, or shorter than, 3A. Veins M_3 and Cu_1 are connate or approximate at their origins, except in *Culapa* (Fig. 104) where they are widely separated, and M_2 arises much nearer M_1 than M_3.

The pattern is highly variable. Many genera show the greatest development of the ocelli in forewing space Cu_1-Cu_2. Most of the species are dark brown on both surfaces, hence the common name "bushbrowns", but some of the African species are iridescent blue or purple above and the Malgache species *Masoura masoura* (Hewitson) is white with a yellow patch on the forewing, superficially more resembling a pierid than a satyrid. The distribution of androconia is characteristic: there is a polished area along the inner margin of the forewing on the under surface, and other areas of androconial concentration are in the area between Cu_2 and 2A of the forewing
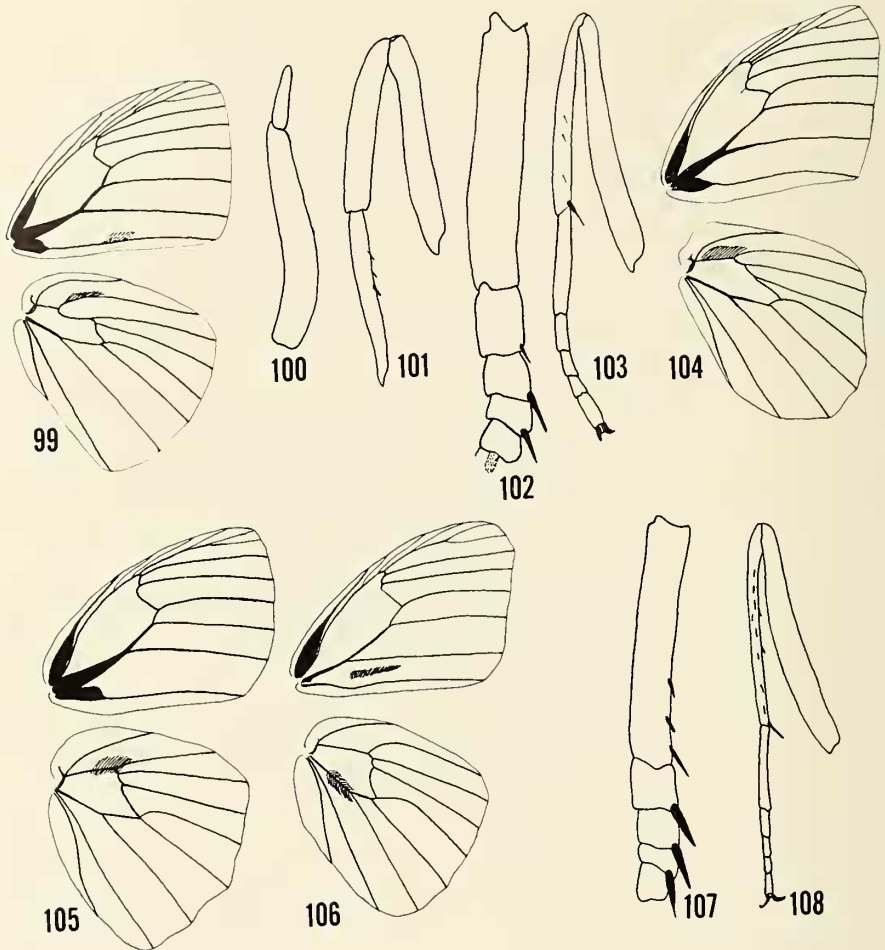
Figs. 99-108. Elymniinae: Mycalesini. 99. *Mycalesis francisca* (Stoll), ♂ venation. 100. *M. francisca*, palpus. 101. *M. francisca*, ♂ foreleg. 102. *M. francisca*, ♀ foretarsus. 103. *M. francisca*, midleg. 104. *Culapa mnasicles* (Hewitson), ♂ venation. 105. *Mydosama fuscum* (Felder and Felder), ♂ venation. 106. *Orsotriaena medus* (Fabricius), ♂ venation. 107. *O. medus*, ♀ foretarsus. 108. *O. medus*, midleg.

and along the hindwing cell on both margins. Hair tufts are more frequent than mealy patches in this tribe.

Genera Included in the Mycalesini

Indo-Australian genera

Bletogona Felder and Felder, 1867 (1864-1867): 465. Type-species: *Bleto-*

gona mycalesis Felder and Felder, by monotypy.

Calysisme Moore, 1880 (1880-1881): 20. Type-species: *Papilio drusia* Cramer, designated by Moore, 1891 (1890-1893): 172.

Celebina Fruhstorfer, 1898: 263. Type-species: *Celebina inga* Fruhstorfer, designated by Hemming, 1935: 1.

Culapa Moore, 1878: 825. Type-species: *Mycalesis mnasicles* Hewitson, by monotypy.

Dalapa Moore, 1880: 158. Type-species: *Mycalesis sudra* Felder, by original designation.

Hamadryopsis Oberthür, 1899: 17. Type-species: *Hamadryopsis drusillodes* Oberthür, by monotypy.

    = *Drusillopsis* Fruhstorfer, 1908: 217. Type-species: *Hamadryopsis drusillodes* Oberthür, by monotypy.

Indalasa Moore, 1880: 166. Type-species: *Mycalesis moorei* Felder, by monotypy.

Jatana Moore, 1880: 164. Type-species: *Mycalesis mynois* Hewitson, by monotypy.

Kabanda Moore, 1880: 168. Type-species: *Mycalesis malsarida* Butler, by original designation.

Loesa Moore, 1880: 177. Type-species: *Mycalesis oroatis* Hewitson, by monotypy.

Lohora Moore, 1880: 175. Type-species: *Mycalesis dexamenus* Hewitson, by original designation.

Martanda Moore, 1880: 169. Type-species: *Mycalesis janardana* Moore, by original designation.

Monotrichtus Hampson, 1891: 179. Type-species: *Mycalesis safitza* Hewitson, by original designation. Originally proposed as a subgenus of *Mycalesis* Hübner.

Mycalesis Hübner, 1818 (1818-1825): 17. Type-species: *Papilio francisca* Stoll, designated by Hemming, 1937: 149. Butler, 1868a: 196, designated *Papilio evadne* Cramer as type, based on *Mycalesis* Hübner, [1819] (1816-1826): 55. This designation was invalidated when the appropriate sections of the "Zuträge" were found to be older than those of the "Verzeichniss".

    = *Gareris* Moore, 1880: 156. Type-species: *Mycalesis sanatana* Moore (= *Papilio francisca* Stoll), by original designation.

Mydosama Moore, 1880: 170. Type-species: *Dasyomma fuscum* Felder and Felder, by original designation.

    = *Dasyomma* Felder and Felder, 1860: 401. Type-species: *Dasyomma fuscum* Felder and Felder, by monotypy. Preoccupied by *Dasyomma* Macquart, 1841.

Myrtilus deNicéville, 1891: 341. Type-species: *Mycalesis (Myrtilus) mystes* deNicéville, by original designation. Proposed as a subgenus of *Mycalesis* Hübner.
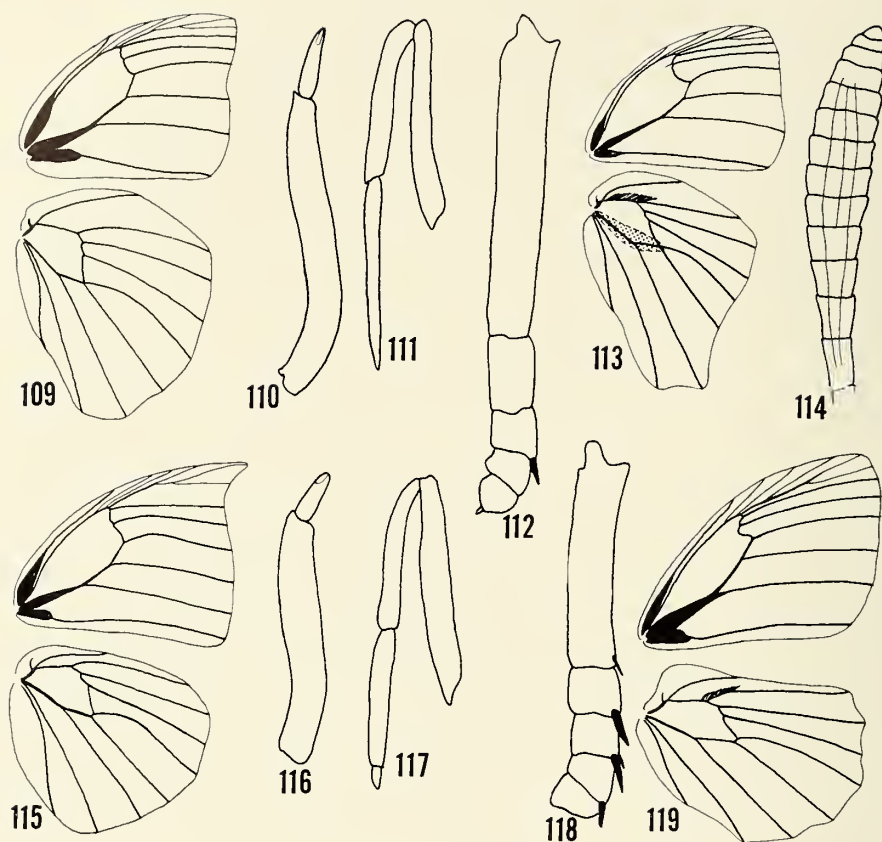
Figs. 109-119. Elymniinae: Mycalesini. 109. *Bicyclus hewitsonii* (Doumet), ♂ venation. 110. *B. hewitsonii*, palpus. 111. *B. hewitsonii*, ♂ foreleg. 112. *B. hewitsonii*, ♀ foretarsus. 113. *Dichothyris sambulos* (Hewitson), ♂ venation. 114. *Heteropsis drepana* Westwood, antennal club. 115. *H. drepana*, ♂ venation. 116. *H. drepana*, palpus. 117. *H. drepana*, ♂ foreleg. 118. *H. drepana*, ♀ foretarsus. 119. *Admiratio paradoxa* (Mabille), ♂ venation.

Nasapa Moore, 1880: 176. Type-species: *Mycalesis aramis* Hewitson, by monotypy.

Nebdara Moore, 1880: 173. Type-species: *Mycalesis tagala* Felder, by original designation.

Nissanga Moore, 1880: 169. Type-species: *Mycalesis patnia* Moore, by original designation.

Orsotriaena Wallengren, 1858: 79. Type-species: *Papilio medus* Fabricius (= *Papilio hesione* Cramer), by monotypy.

Pachama Moore, 1880: 165. Type-species: *Mycalesis mestra* Hewitson, by monotypy.

Physcon deNicéville, 1898: 133. Type-species: *Mycalesis pandoea* Hopffer, by original designation. Proposed as a subgenus of *Mycalesis* Hübner.

Sadarga Moore, 1880: 157. Type-species: *Mycalesis gotama* Moore, by original designation.

Samundra Moore, [1890-1892] (1890-1893): 162. Type-species: *Mycalesis anaxioides* Marshall and deNicéville, by monotypy.

Satoa Moore, 1880: 157. Type-species: *Mycalesis maianeas* Hewitson, by monotypy.

Sevanda Moore, 1880: 174. Type-species: *Satyrus duponcheli* Guérin, by original designation.

Suralaya Moore, 1880: 159. Type-species: *Mycalesis oreseis* Hewitson, by monotypy.

Telinga Moore, 1880: 167. Type-species: *Satyrus adolphei* Guérin, by monotypy.

Virapa Moore, 1880: 156. Type-species: *Mycalesis anaxias* Hewitson, by original designation.

African genera

Bicyclus Kirby, 1871a: 47. Type-species: *Idiomorphus hewitsonii* Doumet, designated by Kirby, 1871b: 363.
> = *Idiomorphus* Doumet, 1861: 174. Type-species: *Idiomorphus hewitsonii* Doumet, by monotypy. Preoccupied by *Idiomorphus* Chaudoir, 1846.

Dichothyris Karsch, 1893: 203. Type-species: *Mycalesis sambulos* Hewitson, designated by Hemming, 1935: 1.

Hallelesis Condamin, 1960: 1257. Type-species: *Mycalesis asochis* Hewitson, designated by Condamin, 1961: 783.

Malgache genera

Admiratio Hemming, 1964b: 137. Type-species: *Smithia paradoxa* Mabille, by original designation.
> = *Smithia* Mabille, 1880: 173. Type-species: *Smithia paradoxa* Mabille, by monotypy. Preoccupied by *Smithia* Milne Edwards and Haime, 1851.

Henotesia Butler, 1879: 228. Type-species: *Henotesia wardii* Butler, by original designation.

Heteropsis Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852: 323. Type-species: *Heteropsis drepana* Westwood, by monotypy.

Houlbertia Oberthür, 1916: 199. Type-species: *Erebia passandava* Ward, designated by Hemming, 1964a: 120.

Masoura Hemming, 1964b: 138. Type-species: *Melanitis masoura* Hewitson, by original designation.
> = *Gallienia* Oberthür, 1916: 205. Type-species: *Melanitis masoura* Hewitson, designated by Hemming, 1964a: 120.

Subfamily ERITINAE, new subfamily

It is obvious that the two genera in this subfamily are intermediate between the Elymniinae (and closest to the Lethini of that subfamily) and the Satyrinae, but perhaps the present genera should not be combined into a single sub-family or tribe. Nevertheless, these genera seem closest to one another, and I should be reluctant to erect two monotypic taxa for them.

The female foretarsus is pentamerous and unclubbed (Figs. 125, 131) and more primitive than that of the Satyrinae. The pattern is rather more primitive than that of most satyrines (Schwanitsch, 1924) and more closely approximates the pattern of the lethines. The male foreleg of the genus *Coelites* is much reduced over the situation in the lethines, however, and the forewing cell of *Erites* is much longer than that of any elymniine.

Both genera are found on the Malay peninsula and in Indonesia. A single tribe, the Eritini, includes all species.

Tribe ERITINI, new tribe

(Figures 120-132)

The diagnostic features of the subfamily Eritinae and of the only tribe, the Eritini, are as follows:

The eyes are naked. The antennae are about two-fifths the length

Fig. 120. Eritinae: Eritini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of the genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

of the forewing costa. The antennal club is indistinct (*Coelites,* Fig. 122) to gradual (*Erites,* Fig. 128) and never more than twice as thick as the shaft. The third segment of the palpus is about

one-fifth as long as the second, and the development of the hairs of the second segment is variable: in *Coelites* they are about as long as the segment is wide, whereas in *Erites* the hairs are two and a half times the width of the segment.

The male foreleg is variably developed: that of *Erites* is slightly miniaturized with subequal femur and tibia and a monomerous, unspined tarsus (Fig. 130); whereas that of *Coelites* is greatly reduced, the femur longer than the tibia and the tarsus represented only by a bump at the tip of the tibia (Fig. 124). The female foreleg is moderately well developed with a pentamerous, unclubbed tarsus bearing spines on the third and fourth subsegments (*Erites*, Fig. 131) or on the first four subsegments (*Coelites*, Fig. 125). The midlegs are approximately equal to, or slightly longer than, the hindlegs (Fig. 120). The midtibia is just over twice as long as the first midtarsal subsegment and is smooth dorsad with moderately well developed tibial spurs and no spines at the dorsal, distal end.

The forewing cell is produced at the origin of M_1 and one-half (*Coelites*, Fig. 121) to three-fifths (*Erites*, Fig. 127) as long as the forewing costa. The forewing radial veins arise in three branches from the cell, and Rs and M_1 are approximate. Vein M_2 arises slightly nearer (*Erites*) to much nearer (*Coelites*) M_1 than M_3, and Cu_1 arises somewhat nearer M_3 than Cu_2. Only forewing vein Sc is inflated basad.

The hindwing cell is produced at the origin of M_3 and is less than half (*Coelites*, Fig. 121) to three-fifths (*Erites*, Fig. 127) as long as the wing measured to the end of M_3. Hindwing vein $Sc+R_1$ is longer than 3A, and veins M_3 and Cu_1 may be connate (*Coelites*) to widely separated (*Erites*) at their origins. Vein M_2 arises slightly nearer M_1 than M_3.

Erites is an olive-brown insect above with the lines of the under surface faintly indicated and ocelli in forewing spaces M_1-M_2, M_2-M_3 and a large one in Cu_1-Cu_2 and hindwing spaces Rs-M_1 through Cu_1-Cu_2. On the under surface the pattern is the same but there are dark striations and transverse ochre lines in the medial areas of both wings. *Coelites* is uniform gray-brown above with a basal purplish sheen and a patch of oily hairs between hindwing veins 2A and 3A. The under surface is dark brown basad, gray-brown mar-
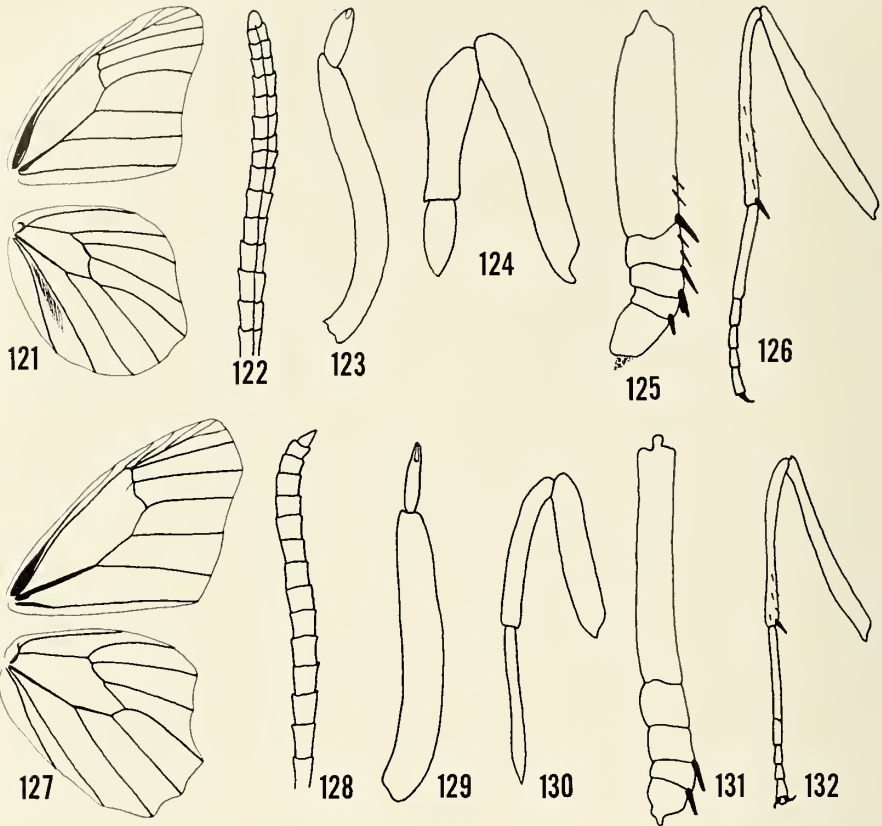
Figs. 121-132. Eritinae: Eritini. 121. *Coelites nothis* Westwood and Hewitson, ♂ venation. 122. *C. nothis*, antennal club. 123. *C. nothis*, palpus. 124. *C. nothis*, ♂ foreleg. 125. *C. nothis*, ♀ foretarsus. 126. *C. nothis*, midleg. 127. *Erites madura* (Horsefield), ♂ venation. 128. *E. madura*, antennal club. 129. *E. madura*, palpus. 130. *E. madura*, ♂ foreleg. 131. *E. madura*, ♀ foretarsus. 132. *E. madura*, midleg.

ginad with ocelli in hindwing spaces Rs-M_1 through Cu_1-Cu_2.

Genera Included in the Eritini

Coelites Westwood and Hewitson, 1850, *in* Doubleday, Westwood and Hewitson, 1846-1852: pl. 66. Type-species: *Coelites nothis* Westwood and Hewitson, designated by Butler, 1868a: 195.

Erites Westwood, 1850, *in* Doubleday, Westwood and Hewitson, 1846-1852: 392. Type-species: *Hipparchia madura* Horsefield, by monotypy.

Subfamily RAGADIINAE Herrich-Schäffer, 1864

Ragadiina Herrich-Schäffer, 1864: 124.

It is difficult to place the Ragadiinae in a satisfactory systematic position, but for reasons to be enumerated below, this subfamily appears to occupy a position intermediate between the Elymniinae and the Satyrinae. In common with the former, hindwing veins M_3 and Cu_1 arise from a common point on the cell, but the abortion of the forelegs of both sexes (Figs. 136, 137) is a characteristic shared with the Satyrinae and *Coelites* of the Eritinae. In other respects, however, the ragadiines stand apart from all of the other subfamilies.

The configuration of the hindwing cell (Figs. 134, 139) is distinctive. In males the cell is closed by narrow vestigial veins, whereas in the females of some species the cell is completely open between the origins of veins M_2 and M_3.

All members of the Ragadiinae are native to the Indo-Australian region and constitute a single tribe, the Ragadiini. Röber (1892) split this subfamily, referring *Acrophtalmia* to the *Ypthima* group and *Ragadia* to the *Mycalesis* group, but the characteristic venation of the hindwing cannot be ascribed merely to the convergence of two different phyletic lines.

Tribe RAGADIINI Herrich-Schäffer, 1864

(Figures 133-139)
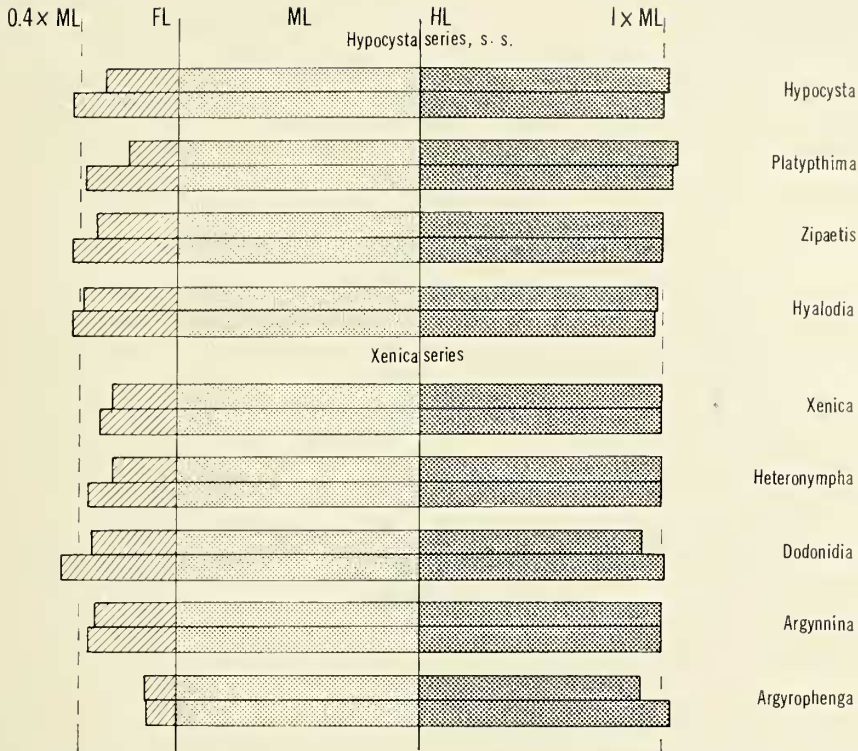
Ragadiina Herrich-Schäffer, 1864: 124.
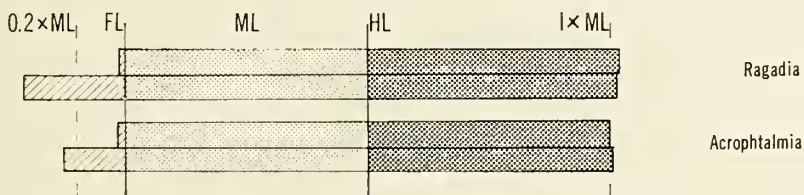
Fig. 133. Ragadiinae: Ragadiini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.
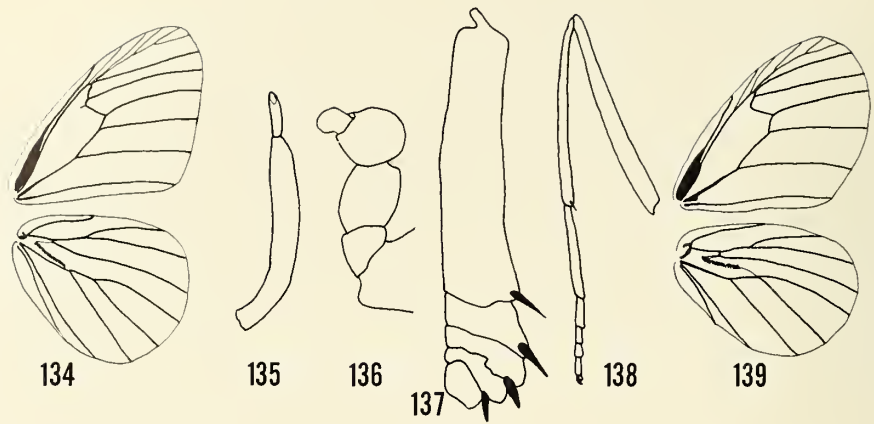
Figs. 134-139. Ragadiinae: Ragadiini. 134. *Ragadia crisia* (Geyer), ♂ venation. 135. *R. crisia*, palpus. 136. *R. crisia*, ♂ foreleg, showing also the trochanter and the distal portion of the coxa. 137. *R. crisia*, ♀ foretarsus. 138. *R. crisia*, midleg. 139. *Acrophtalmia artemis* Felder and Felder, ♂ venation.

The diagnostic features of the subfamily Ragadiinae and its only tribe, the Ragadiini, are as follows:

The eyes are naked. The antennae are no more than half the length of the forewing costa. The antennal club is moderately well developed, occupies the distal one-fourth to two-fifths of the antenna and is thickened to two and a half to three times the width of the shaft. The third segment of the palpus is from less than a quarter (*Ragadia*) to slightly less than one-third (*Acrophtalmia*) the length of the second segment. The hairs of the second segment of the palpus are shorter than the segment is wide.

The male foreleg is greatly reduced with but a bump representing the tarsus in some species (*Ragadia*, Fig. 136, for example); the tarsus is completely fused with the tibia and indistinguishable from it in *Acrophtalmia*. The femur and tibia are of about the same length. The female foreleg is also miniaturized and the tarsus clubbed with five subsegments bearing spines on the first four. The mid- and hindlegs are of about the same length. The midtibia is less than twice the length of the first midtarsal subsegment, is smooth dorsad and bears weakly developed tibial spurs, but no spine at the dorsal, distal end. The relative lengths of the legs are shown in Fig. 133.

The forewing cell is excavate near the origin of M₂ and about

three-fifths the length of the forewing costa. The forewing radial veins arise in two branches from the cell, and veins Rs and M_1 are nearly connate. Vein M_2 arises nearer M_1 than M_3, and Cu_1 arises much nearer M_3 than Cu_2. Forewing vein Sc is inflated basad, but the other veins are not.

The hindwing cell is distinctive. It is open in some females and at most closed by small, aberrant veins (Figs. 134, 139). The cell is from less than half (*Acrophtalmia*) to more than three-fifths (*Ragadia*) as long as the wing measured to the end of M_3. The relative lengths of hindwing veins $Sc + R_1$ and 3A vary: $Sc + R_1$ is longer in *Acrophtalmia,* and 3A is longer in *Ragadia*. Veins M_3 and Cu_1 are connate, whereas M_2 arises *basad* of M_1 and much closer to it than to M_3.

The pattern is highly modified, either brown with a broad central white band or with alternating brown and off-white stripes. The ocelli are poorly developed, except in *Ragadia* which has a full complement on the under surface. An androconial hair tuft lies on the aberrant veins of the hindwing cell (Figs. 134, 139) and is characteristic of the tribe.

Genera Included in the Ragadiini

Acrophtalmia Felder and Felder, 1861: 305. Type-species: *Acrophtalmia artemis* Felder and Felder, by monotypy. Many authors, following Felder and Felder, 1867 (1864-1867): 486, have misspelled this name "*Acrophthalmia*".

Acropolis Hemming, 1934b: 77. Type-species: *Acrophthalmia* (*sic.*) *thalia* Leech, by original designation.

     = *Pharia* Fruhstorfer, 1912 (1912-1915): 295. Type-species: *Acrophthalmia* (*sic.*) *thalia* Leech, by monotypy. Preoccupied by *Pharia* Gray, 1840.

Ragadia Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852: 376. Type-species: *Euptychia crisia* Geyer, by monotypy. Proposed as a subgenus of *Neonympha* Hübner.

Subfamily SATYRINAE Boisduval, 1836

Satyrides Boisduval, 1836: 166; Satyridae Swainson, 1840: 86.
= Hipparchiadae Kirby, 1837: 297.
= Maniolinae Hampson, 1918: 385.

The Satyrinae are the most evolved members of the family and

TABLE 6

Some of the diagnostic characters of the tribes of the Satyrinae.

Character	Hypocystini	Ypthimini	Euptychiini	Coenonymphini
Length of hindwing cell: length of wing	1/2-3/5	3/5	1/2-3/5	1/2-3/5
Ratio of lengths of midtibia to 1st midtarsus	1.5->2	1.5-2	1.5-1.75	Gen. >2
♀ foretarsus	Pentamerous, sl. clubbed	Pentamerous, clubbed	Pentamerous, clubbed	Monomerous or tetramerous, gr. reduced
Midtibia dorsad	Smooth	Smooth	Gen. smooth	Smooth
Inflation of the forewing veins	Sc always, others in various genera	Sc, Cu only	Sc, Cu always, occasionally 2A	Sc. Cu, 2A all
Forewing radial veins	2 or 3 stems	1 or 2 stems	2 stems, rarely 1	2 stems, rarely 3
Antennal club development	Gen. well developed	Variously developed	Weakly developed	Weakly to v. strongly developed

TABLE 6. (*Continued*)

Character	Maniolini	Erebiini	Dirini	Pronophilini	Satyrini	Melanargiini
Length of hindwing cell: length of wing	1/2-3/5	1/2-3/5	<1/2	1/2->3/5	1/2-3/5	1/2-3/5
Ratio of lengths of midtibia to 1st midtarsus	1.75-2	ca. 1.5	<1.25 or >2	Gen. 2	Gen. 1.25	ca. 1.5
♀ foretarsus	Monomerous or dimerous, gr. reduced	Dimerous to pentamerous, clubbed	Monomerous or dimerous, gr. reduced	Gen. penta-merous, clubbed	Monomerous to tetramerous, gr. reduced	Monomerous, gr. reduced
Midtibia dorsad	Smooth	Gen. smooth	V. spiny; some spp. with a distal spine	Gen. very spiny	Very spiny, most spp. with a spine distad	Very spiny
Inflation of the forewing veins	Se always, occasionally Cu and 2A	Se always, Cu slightly	Sc only and slightly	Se always, occasionally Cu and 2A	Se always, Cu and 2A only slightly	Se only
Forewing radial veins	3 stems	3 stems	3 stems	3 stems, rarely 2 or 1	3 stems	3 stems
Antennal club development	Weakly developed	Well developed	Well developed	Well developed	Well developed	Weakly developed

have become the dominant group throughout most of the world. Fairly close relationships with three other subfamilies, the Elymniinae, Eritinae and Ragadiinae, are indicated by analysis of structures, and there are three instances of gradation between the elymniines and the satyrines. There is probably only convergence between the *Aeropetes*-series of the Lethini and the Dirini of the present subfamily. Far more significant evolutionarily, however, are such genera as *Lamprolenis* in the primitive satyrine tribe Hypocystini. These butterflies show certain similarities to some Mycalesini and Lethini (*Mandarinia*) of the Elymniinae, particularly as regards pattern and the placement of the androconial areas. This is probably the stock from which the Satyrinae evolved. The Lethini are connected to the Satyrinae through the sub-family Eritinae, as indicated in the discussion of the eritines. This evidence seems to place the Lethini as the closest present-day ancestral stock of the Satyrinae. The relationship with the ragadiines is obscure and more in the nature of an association because of the greatly reduced forelegs of both sexes.

Any satyrid with fewer than five subsegments on the female foretarsus is a member of this subfamily. Even when there are five subsegments on the female foreleg of a member of the present subfamily, the tarsus is formed into a clublike structure totally unlike anything found in the Haeterinae, Brassolinae, Biinae, Elymniinae or Eritinae, but hinted at in the Ragadiinae. Comparative female foretarsi of the pentamerous type are shown in Figs. 5 (Haeterinae), 15 (Brassolinae), 24, 32 (Biinae), 52, 84, 95, 102 (Elymniinae), 131 (Eritinae), 137 (Ragadiinae) and 145, 174, 200 (Satyrinae). A greatly reduced male foreleg will serve to separate the Satyrinae from all other satyrid subfamilies except the Ragadiinae and *Coelites* of the Eritinae. None of the satyrines have the hindwing veins M_3 and Cu_1 connate, nor the open hindwing cell of the ragadiines. The hindwing cell, measured to the origin of vein M_3, is greater than half as long as the wing to the end of M_3, except in some Dirini. The antennal club is always moderately well and frequently highly developed.

The Satyrinae are virtually cosmopolitan, with representatives in all parts of the world where butterflies are found, except some oceanic islands. Unlike the other subfamilies, the Satyrinae are highly developed in temperate regions.

Ten tribes are recognized in the Satyrinae. The most primitive

tribe, the Hypocystini, contains genera which span the gap between the other two groups. The Ypthimini-section, characterized more or less by their smaller size, frailer appearance and an ecological preference for grasslands, contains the tribes Ypthimini, Euptychiini, Coenonymphini, Maniolini and Erebiini. The Satyrini-section, larger and sturdier insects with woodland or scrubland preferences, is composed of the tribes Dirini, Pronophilini, Satyrini and Melanargiini. A key to the tribes of the Satyrinae is given below, and a diagnostic chart of these tribes is provided in Table 6.

KEY TO THE TRIBES OF THE SATYRINAE

1. Hindwing cell half or less the length of the wing; forewing cell rounded distad (Figs. 248, 255, 256); South Africa .... Dirini
   Hindwing cell greater than half the length of the wing; forewing cell square-cut or excavate 2
2. Midtibia with a long spine at the dorsal distal end (Fig. 301); Holarctic .... most Satyrini
   Midtibia without such a spine 3
3. Hindwing cell prolonged by a distad displacement of crossvein m_2-m_3 along vein M_2 (Fig. 261, for example) 4
   Hindwing cell more or less square cut with crossvein m_2-m_3 in line with m_1-m_2 (Fig. 309, for example) 8
4. Female foretarsus with fewer than five subsegments 5
   Female foretarsus pentamerous 6
5. Third segment of palpus less than one-fourth the length of the second (Fig. 305); Holarctic .... Satyrini (*Oeneis*-series)
   Third segment of palpus longer than one-fourth the length of the second (Fig. 282); Neotropical .... some Pronophilini
6. Midtibia spiny; Neotropics .... most Pronophilini
   Midtibia smooth 7
7. Neotropical species .... a few Pronophilini
   Australian region species .... Hypocystini
8. White (or cream-colored) species, marbled with
      black; Palearctic .... Melanargiini
   Generally brown or orange species, if white
      not marbled 9
9. Female foretarsus with fewer than five subsegments 10
   Female foretarsus pentamerous 12
10. Forewing veins only slightly inflated (Figs.
       234, 240); Holarctic .... Erebiini
    Forewing veins inflated (Fig. 224, for example) 11

11. Midtibia twice or more the length of the first
    midtarsal subsegment; Holarctic .... Coenonymphini
    Midtibia less than twice as long as the first
    midtarsal subsegment; Holarctic .... Maniolini
12. Forewing with a double-pupilled ocellus in space
    M_1-M_2 or M_1-M_3; Old World 13
    Forewing with no ocellus in space M_1-M_3, or if
    present only single-pupilled; New World .... Euptychiini
13. Eyes naked .... Ypthimini
    Eyes hairy .... genus *Palaeonympha*

Tribe HYPOCYSTINI, new tribe

(Figures 140-169)

The Hypocystini are here considered to be the most primitive members of the Satyrinae, primarily because of the configurations of the male and female forelegs. Although these butterflies are not closely allied to any other tribe within the Satyrinae, they seem to connect the Ypthimini- and Satyrini-sections. The *Xenica*-series in the present tribe connects with the Satyrini-section by pattern and structural similarities, whereas the *Hypocysta*-series exhibits an even closer approach to the Ypthimini-section. The New Guinean hypocystine genus *Lamprolenis* shows many characteristics in common with the elymniine tribes Mycalesini and Lethini. This genus has the typical mycalesine androconial patch along the anterior portion of the hindwing, and the general facies are reminiscent of the mycalesines or of *Mandarinia*. This similarity may offer an explanation of the evolution of the Satyrinae and will be discussed in greater detail later.

Parallel evolution is shown very well by the New Zealand members of this tribe, with the exception of *Dodonidia*. The other members, living in montane situations, have evolved into butterflies very like the Holarctic genus *Erebia*—indeed, several were placed in that genus by early authors. Because the New Zealand "coppers" are placed in the Holarctic genus *Lycaena* Fabricius (H. K. Clench, personal communication), the possibility that *Argyrophenga* and especially *Erebiola* and *Percnodaimon* are indeed referable to *Erebia* had to be examined, but there is no morphologic evidence to support their inclusion in the Holarctic genus. The New Zealand *"Erebia"* . are highly modified Hypocystini, most nearly related to the Australian members of the tribe.

Fig. 140. Satyrinae: Hypocystini. Relative lengths of the femur +
tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stip-
pling) and hindlegs (HL, heavy stippling) of selected genera. In all instances
the ML value is unity. The top bar for each genus represents the measurements
obtained from males, the bottom bar those from females.

Members of the New Guinean hypocystine fauna (*Platypthima,
Erycinidia, Pieridopsis* and *Lamprolenis*) have evolved into bewil-
dering butterflies. In fact, in wing shape and general appearance
Erycinidia is a classic riodinid, and *Pieridopsis* is a fine pierid
"mimic".

The less miniaturized forelegs in both sexes serves to distinguish
the hypocystines from all other Satyrinae. The forewing cell is usually
deeply excavate in this tribe, a characteristic shared with such
Ypthimini-section tribes as the Ypthimini and Coenonymphini, but
the hindwing crossvein m_2-m_3 is produced marginad along M_2, as
in much of the Satyrini-section. Forewing vein 2A is usually inflated
basad, recalling the Mycalesini, but the inflated part is not sub-

quadrate in the hypocystines. A few of the *Xenica*-series have little
or no inflation of forewing vein 2A.

All members of the Hypocystini are found in the Australian
region, a few being found as far west as Indonesia. Most of the
species are found in New Zealand, Australia, New Guinea and the
associated oceanic islands. Two series of genera are recognized.
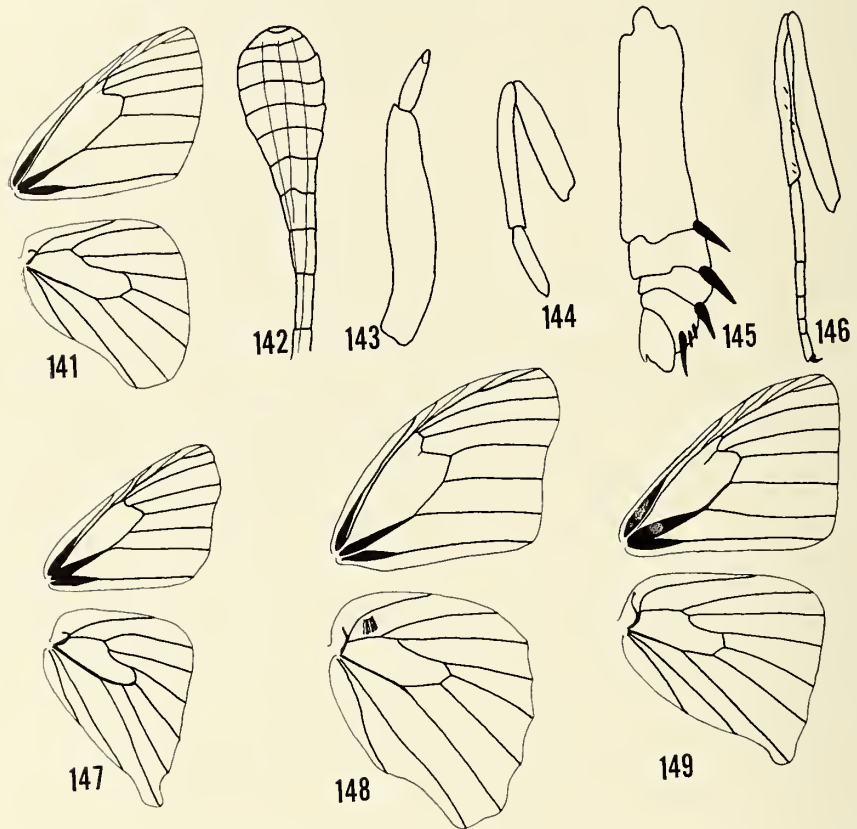
Figs. 141-149. Satyrinae: Hypocystini. 141. *Hypocysta euphemia* West-
wood and Hewitson, ♂ venation. 142. *H. euphemia*, antennal club. 143. *H.
euphemia*, palpus. 144. *H. euphemia*, ♂ foreleg. 145. *H. euphemia*, ♀ fore-
tarsus. 146. *H. euphemia*, midleg. 147. *Erycinidia gracilis* Rothschild and
Jordan, ♂ venation. 148. *Lamprolenis nitida* Godman and Salvin, ♂ vena-
tion. 149. *Pieridopsis virgo* Rothschild and Jordan, ♂ venation.

The *Hypocysta*-series, *sensu stricto*, most of which are exclusively
tropical insects, are characterized by the generally absent tibial spurs,

the longer third segment of the palpus and hindwing vein M_2 arising nearer M_3 than M_1.

The *Xenica*-series is restricted to the temperate part of the region and characterized by the development of the tibial spurs, the shorter third segment of the palpus and (in many genera) hindwing vein M_2, which arises midway between M_1 and M_3.

The Hypocystini are characterized as follows:

The eyes are generally naked, although they are hairy in such diverse genera as *Argynnina, Heteronympha, Nesoxenica* and *Platypthima*. The antennae are generally two-fifths to half the length of the forewing costa, but the antennae of *Argyronympha* are three-fifths the length of the costa. The antennal club is well developed in most genera, occupying the distal one-fifth to one-third of the antenna and expanded to three to four times the width of the shaft (just over twice the width of the shaft in *Lamprolenis*). The club is eccentrically developed in some New Zealand genera (Figs. 163, 166, 169). The third segment of the palpus is variously one-half to one-third the length of the second in the *Hypocysta*-series (Fig. 143) and one-fourth to one-fifth the length of the second in the *Xenica*-series (Fig. 157). The hairs of the second segment of the palpus vary from less than the width of the segment to more than twice as long as the segment is wide in the *Hypocysta*-series to over four times the width of the segment in some of the New Zealand genera.
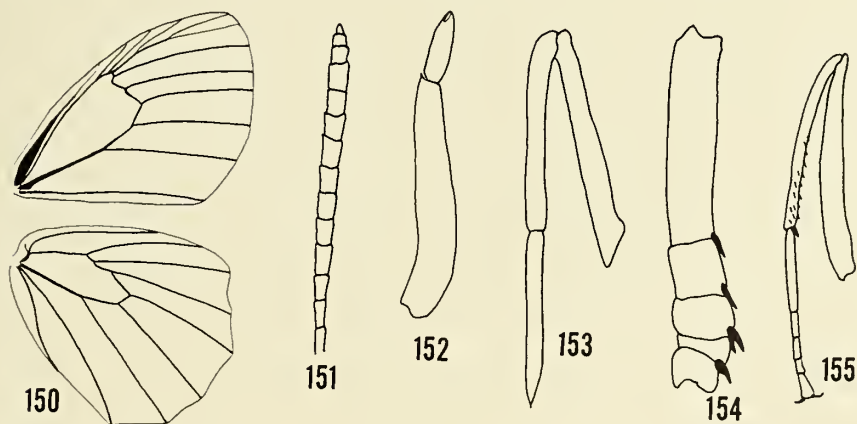
Figs. 150-155. Satyrinae: Hypocystini, all *Zipaetis saitis* Hewitson. 150. ♂ venation. 151. antennal club. 152. palpus. 153. ♂ foreleg. 154. ♀ foretarsus. 155. midleg.

The male foreleg is moderately well developed (Fig. 140); the tibia is usually longer than the femur, and the tarsus is usually monomerous, but may have as many as four subsegments. The female foreleg is also well developed (Fig. 140) with a pentamerous, only slightly clubbed tarsus bearing spines on the first four subsegments (Fig. 145, for example)—there are more than one pair of spines on each of the first four subsegments in *Dodonidia* (Fig. 164). The midlegs are as long as, or longer than, the hindlegs (Fig. 140). The midtibia is from less than twice to more than twice the length of the first midtarsal subsegment, and the tibia is smooth dorsad. Tibial spurs are generally well developed in the *Xenica*-series (Fig. 160), including the New Zealand genera; but the spurs are generally absent in the *Hypocysta*-series (Fig. 146), but they are weakly developed in *Pieridopsis* and moderately developed in *Zipaetis* (Fig. 155). No spine is developed on the dorsal, distal end of the midtibia.

The forewing cell is excavate, often deeply so, and is from more than half to more than three-fifths the length of the forewing costa. In the *Hypocysta*-series, *Argyrophenga* and *Dodonidia* the forewing radial veins arise in two branches from the cell; in the other genera the radials arise in three branches. Forewing veins Rs and M_1 are connate in *Argyrophenga, Erebiola* and *Percnodaimon,* and separate, though often approximate, in the other genera. Vein M_2 arises nearer, often much nearer, M_1 than M_3, and Cu_1 arises a little nearer M_3 than Cu_2. Vein Sc is characteristically inflated in all genera but *Dodonidia* (Fig. 162), and the cubital stem and 2A are inflated in such diverse genera as *Argyrophenga* (Fig. 167), *Xenica* (Fig. 156), *Geitoneura* (Fig. 161) and most of the *Hypocysta*-series (Fig. 141, for example).

The hindwing cell is usually produced at m_2-m_3, but it is more blunted in *Dodonidia* (Fig. 162) and *Zipaetis* (Fig. 150), and the cell is usually half to three-fifths the length of the wing measured to the origin and end of M_3, respectively. The relative lengths of the hindwing veins Sc + R_1 and 3A are variable. Veins M_3 and Cu_1 arise separately, and M_2 commonly arises midway between M_1 and M_3, but nearer the latter in the New Zealand *"Erebia"* and the *Hypocysta*-

Figs. 156-169. Satyrinae: Hypocystini. 156. *Xenica achanta* (Donovan), ♂ venation. 157. *X. achanta,* palpus. 158. *X. achanta,* ♂ foreleg. 159. *X. achanta,* ♀ foretarsus. 160. *X. achanta,* midleg. 161. *Geitoneura klugii*
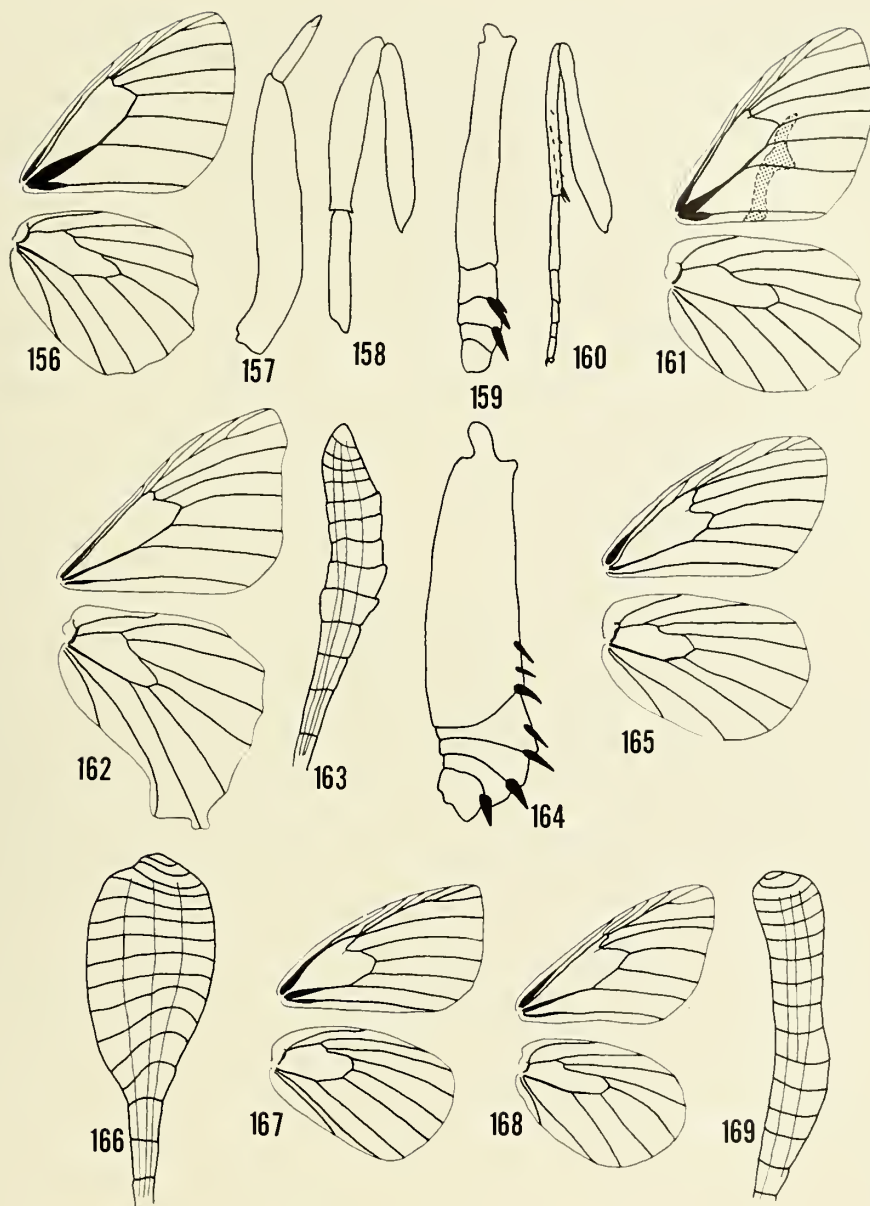
(Guérin), ♂ venation. 162. *Dodonidia helmsii* Butler, ♂ venation. 163. *D. helmsii,* antennal club. 164. *D. helmsii,* ♀ foretarsus. 165. *Percnodaimon pluto* (Fereday), ♂ venation. 166. *P. pluto,* antennal club. 167. *Argyrophenga antipodum* Doubleday, ♂ venation. 168. *Erebiola butleri* Fereday, ♂ venation. 169. *E. butleri,* antennal club.

series.

The pattern is variable and highly modified. Many of the species are illustrated by Waterhouse and Lyell (1914) and by Fruhstorfer (1912[1912-1915]). There is a remarkable resemblance between *Percnodaimon*, *Erebiola* and *Argyrophenga* and the Holarctic *Erebia*.

Genera Included in the Hypocystini

Hypocysta-series, *sensu stricto*

Argyronympha Mathew, 1886: 346. Type-species: *Argyronympha pulchra* Mathew, designated by Hemming, 1943: 23.

Erycinidia Rothschild and Jordan, 1905: 457. Type-species: *Erycinidia gracilis* Rothschild and Jordan, by monotypy.

Harsiesis Fruhstorfer, 1912(1912-1915): 299. Type-species: *Hypocysta hygeia* Hewitson, by monotypy.

Hyalodia Jordan, 1924: 285. Type-species: *Hypocysta tenuisquamosa* Joicey and Talbot, by monotypy.

Hypocysta Westwood and Hewitson, 1850, *in* Doubleday, Westwood and Hewitson, 1846-1852: pl. 67. Type-species: *Hypocysta euphemia* Westwood and Hewitson, by monotypy.

Lamprolenis Godman and Salvin, 1880: 610. Type-species: *Lamprolenis nitida* Godman and Salvin, by monotypy.

Pieridopsis Rothschild and Jordan, 1905: 457. Type-species: *Pieridopsis virgo* Rothschild and Jordan, by original designation.

Platypthima Rothschild and Jordan, 1905: 458. Type-species: *Platypthima ornata* Rothschild and Jordan, by original designation.

Zipaetis Hewitson, 1863(1856-1876): [100]. Type-species: *Zipaetis saitis* Hewitson, designated by Butler, 1868a: 194. This genus is exceptionally aberrant and is only provisionally placed here.

Xenica-series

Argynnina Butler, 1867d: 165. Type-species: *Lasiommata hobartia* Westwood and Hewitson, designated by Butler, 1868a: 196.

Argyrophenga Doubleday, 1845: 307. Type-species: *Argyrophenga antipodum* Doubleday, by monotypy.

Dodonidia Butler, 1884: 172. Type-species: *Dodonidia helmsii* Butler, by original designation.

Erebiola Fereday, 1879: 128. Type-species: *Erebiola butleri* Fereday, by original designation.

Geitoneura Butler, 1867d: 164. Type-species: *Satyrus klugii* Guérin, designated by Butler, 1868b: 166.

Heteronympha Wallengren, 1858: 78. Type-species: *Papilio merope* Fabricius,
    designated by Butler, 1868a: 195.
        =*Hipparchioides* Butler, 1867c: 125. Type-species: *Papilio merope*
        Fabricius, designated by Butler, 1868b: 99.
Nesoxenica Waterhouse and Lyell, 1914: 35. Type-species: *Lasiommata*
    leprea Hewitson, by original designation.
        = *Xeniconympha* Noricky, 1923: 60. Type-species: *Lasiommata*
        leprea Hewitson, by original designation.
Oreixenica Waterhouse and Lyell, 1914: 41. Type-species: *Lasiommata* (?)
    lathionella Westwood, by original designation.
Paratisiphone Watkins, 1928: 615. Type-species: *Lasiommata lyrnessa* Hewit-
    son, by original designation.
Percnodaimon Butler, 1876: 152. Type-species: *Erebia pluto* Fereday, by
    original designation.
Tisiphone Hübner. [1819](1816-1826): 60. Type species: *Papilio abeona*
    Donovan, designated by Butler, 1868b: 71.
Xenica Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852:
    387. Type-species: *Papilio achanta* Donovan, designated by Scudder,
    1875a: 289.

Tribe YPTHIMINI, new tribe
(Figures 170-188)

    This tribe lies at the base of the Ypthimini-section of the Satyrinae
and seems in some respects to connect with the *Hypocysta*-series of
the last tribe.   In its turn the Ypthimini appears to have given rise
to the Holarctic Erebiini and Coenonymphini and the Neotropical
Euptychiini; the Maniolini were evolved later from a coenonymphine
stock.

    The Ypthimini are generally characterized by a pattern feature:
the forewing ocellus in space M_1-M_3 has a double pupil of white or
bluish-white scales.   Forewing vein 2A is not inflated in the ypthi-
mines, whereas in the Coenonymphini and many Euptychiini this
vein is greatly distended.   While the hindwing crossvein m_2-m_3 is
produced at M_2 in the *Hypocysta*-series, the crossveins are aligned in
this tribe and in other members of the Ypthimini-section, resulting in
a straight cell.   The female foreleg is pentamerous in the present
tribe, a situation which is never found in the coenonymphines and
very rare in either the Maniolini or the Erebiini.
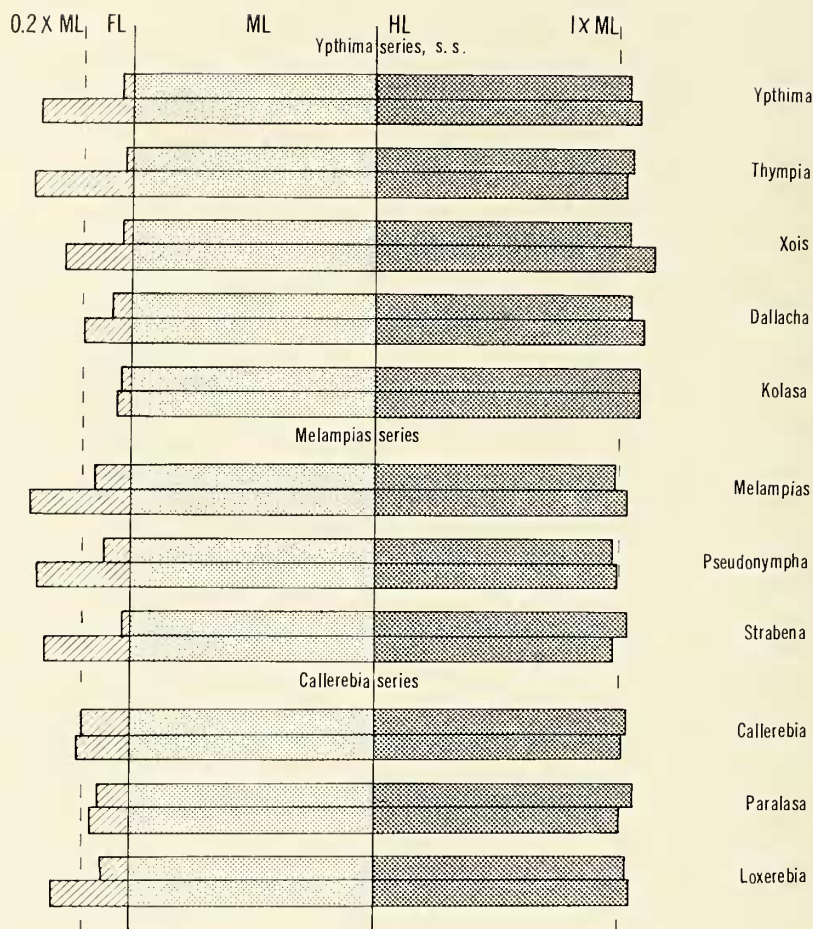
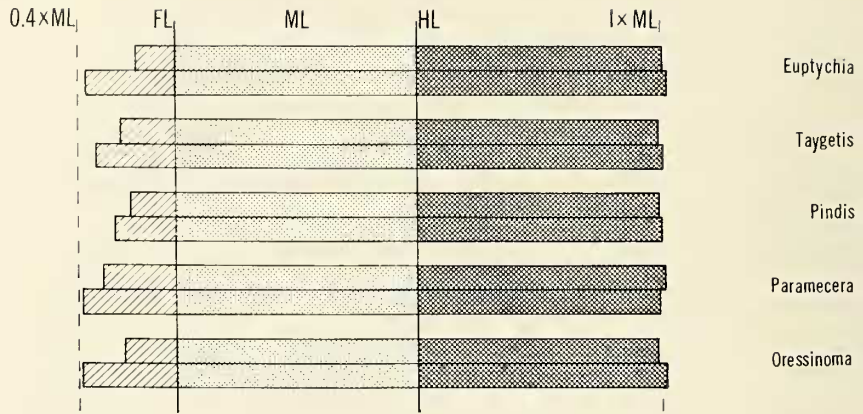Fig. 170. Satyrinae: Ypthimini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

All ypthimines are found in the Old World, and most genera are exclusively tropical. Most species fly in open country; few are found in scrub country, much less in the deep forest. Three major series are recognized in the Ypthimini, as follows:

The *Ypthima*-series, *sensu stricto*, characterized generally by their small size, brown coloration and diffuse androconia. This series is found throughout the Paleotropics.

The *Callerebia*-series, characterized by large size, brown coloration and androconia arranged in rows on the discal portion of the forewing (Fig. 184). These species are generally distributed in the temperate mountains of the Middle and Far East.

The *Melampias*-series, characterized generally by reddish shades on the upper surface, more elongate wings, small size and either diffuse androconia or none. These butterflies are found in South Africa and Madagascar.

The Ypthimini are characterized as follows:

The eyes are naked. The antennae are short, often less than two-fifths the length of the forewing costa (only one-fourth as long in *Mashuna*) and never as long as half the length of the costa (nearly half in *Paralasa* and *Dallacha*). The antennal club is variously developed: in such genera as *Physcaeneura, Periplysia* and *Dallacha* the club is less than twice as thick as the shaft, whereas in genera like *Mashuna* the club is almost four times as thick as the shaft. The third segment of the palpus is usually from one-fourth to slightly over one-third the length of the second, but the third segment is more than half as long as the second segment in *Physcaeneura*. The hairs of the second segment of the palpus are very long, usually three to five times as long as the segment is wide.

The male foreleg is extremely reduced (Fig. 170), with the tarsus represented in most genera by a small knob on the end of the tibia (Fig. 173, for example). In such genera as *Mashuna* (Fig. 177), *Strabena* and *Pandima,* the tarsus is completely fused to the tibia, but in the *Callerebia*-series (Fig. 185) the tarsus is moderately well represented. The forefemur is as long as, or longer than, the foretibia. The female foreleg is also miniaturized, but it retains five tarsal subsegments, but the tarsus itself is significantly clubbed (Fig. 174, for example). There are spines on the second, third and fourth subsegments. The midleg is subequal to the hindleg in the *Callerebia*- and *Melampias*-series, but significantly shorter in the *Ypthima*-series (Fig. 170). The midtibia is less than twice the length of the first midtarsal subsegment, is smooth dorsad, without a spine at the dorsal, distal end and with well to moderately well developed tibial spurs, except in *Physcaenura* (Fig. 179).

The forewing cell is usually produced at the origin of M_3 and not excavate (except in *Periplysia*, Fig. 180); the cell is about half
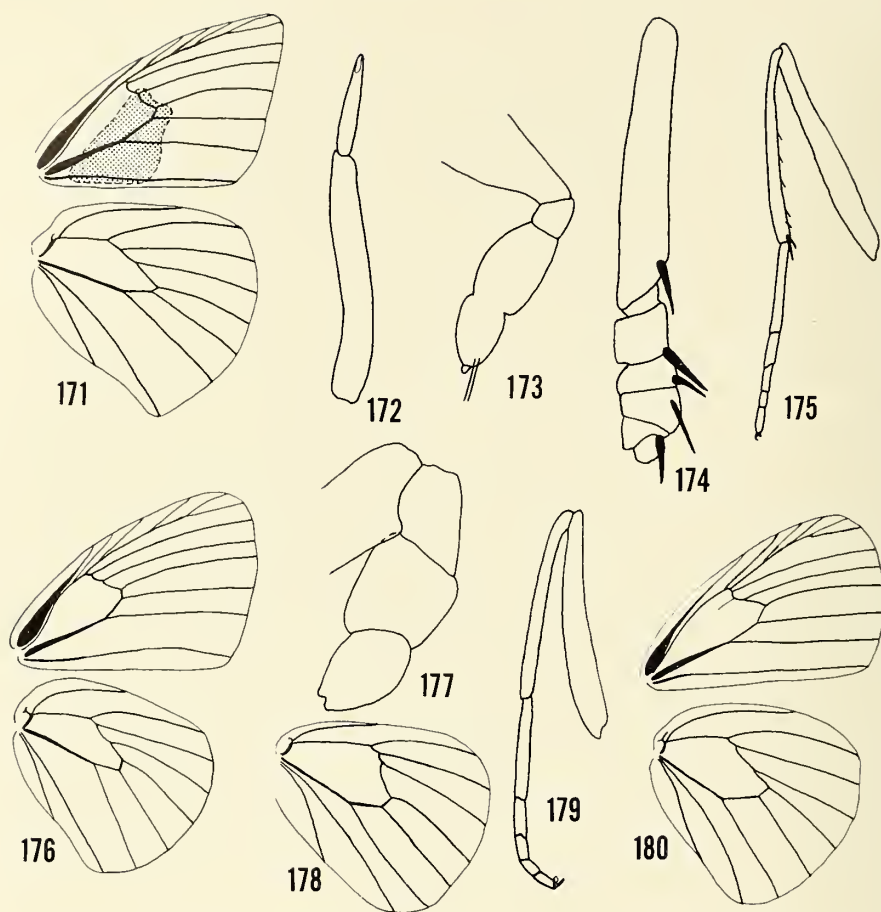
Figs. 171-180. Satyrinae: Ypthimini. 171. *Ypthima philomela* (Linné), ♂ venation. 172. *Y. philomela*, palpus. 173. *Y. phi'omela*, ♂ foreleg, including trochanter and distal portion of coxa. 174. *Y. philomela*, ♀ foretarsus. 175. *Y. philomela*, midleg. 176. *Mashuna mashuna* (Trimen), ♂ venation. 177. *M. mashuna*, ♂ foreleg, including trochanter and distal portion of coxa. 178. *Xois sesara* Hewitson, venation of ♂ hindwing. 179. *Physcaenura panda* (Boisduval), midleg. 180. *P. panda*, ♂ venation.

as long as the forewing costa. The forewing radial veins arise in one or two branches from the cell, and veins Rs and M_1 are well separated at their origins. Vein M_2 usually arises midway between M_1 and M_3, but nearer M_1 in the *Melampias*-series; Cu_1 arises nearer, or much nearer, M_3 than Cu_2. Forewing vein Sc is always much thickened at its base, the cubital stem is generally inflated and 2A never is.

The hindwing cell is straight, longest at the origin of M_3 and is about three-fifths the length of the wing measured to the end of M_3. Hindwing vein $Sc + R_1$ is as long as, and more commonly longer than, 3A. Veins M_3 and Cu_1 arise separately, but often approximate, and M_2 arises somewhat nearer M_1 than M_3, or midway between the two veins.

As noted in the general description, the pattern is rather constant. For illustrations of the various species see Moore (1893[1890-1893]) and van Son (1955).

Genera Included in the Ypthimini

Ypthima-series, sensu stricto

Dallacha Moore, 1893(1890-1893): 94. Type-species: *Yphthima* (*sic.*) *hyagriva* Moore, by original designation.

Hemadera Moore, 1893(1890-1893): 107. Type-species: *Yphthima* (*sic.*) *narasingha* Moore, by original designation.

Kolasa Moore, 1893(1890-1893): 82. Type-species: *Satyrus chenui* Guérin, by original designation.

Lohana Moore, 1893(1890-1893): 92. Type-species: *Yphthima* (*sic.*) *inica* Hewitson, by original designation.

Mashuna van Son, (July) 1955: 159. Type-species: *Ypthima mashuna* Trimen, by original designation.

    = *Ypthimorpha* Overlaet, (Dec.) 1955: 23. Type-species: *Ypthima mashuna* Trimen, by original designation.

Nadiria Moore, 1893(1890-1893): 85. Type-species: *Ypthima bolanica* Marshall, by original designation.

Pandima Moore, 1893(1890-1893): 86. Type-species: *Satyrus nareda* Kollar, by original designation.

Thympia Moore, 1893(1890-1893): 58. Type-species: *Papilio baldus* Fabricius, by original designation.

Xois Hewitson, 1865: 282. Type-species: *Xois sesara* Hewitson, by monotypy.

Ypthima Hübner, 1818(1818-1825): 17. Type-species: *Papilio philomela* Linné, by monotypy. This name is frequently misspelled in the literature as "*Yphthima*". Hemming (1964e: 157-158) makes a strong case for "*philomela*" of Hübner being a misidentification of *Ypthima huebneri* Kirby. Should the International Commission on Zoological Nomenclature rule that this is the case, *Y. huebneri* will become the type-species.

Ypthimomorpha van Son, 1955: 158. Type-species: *Ypthima itonia* Hewitson, by original designation.
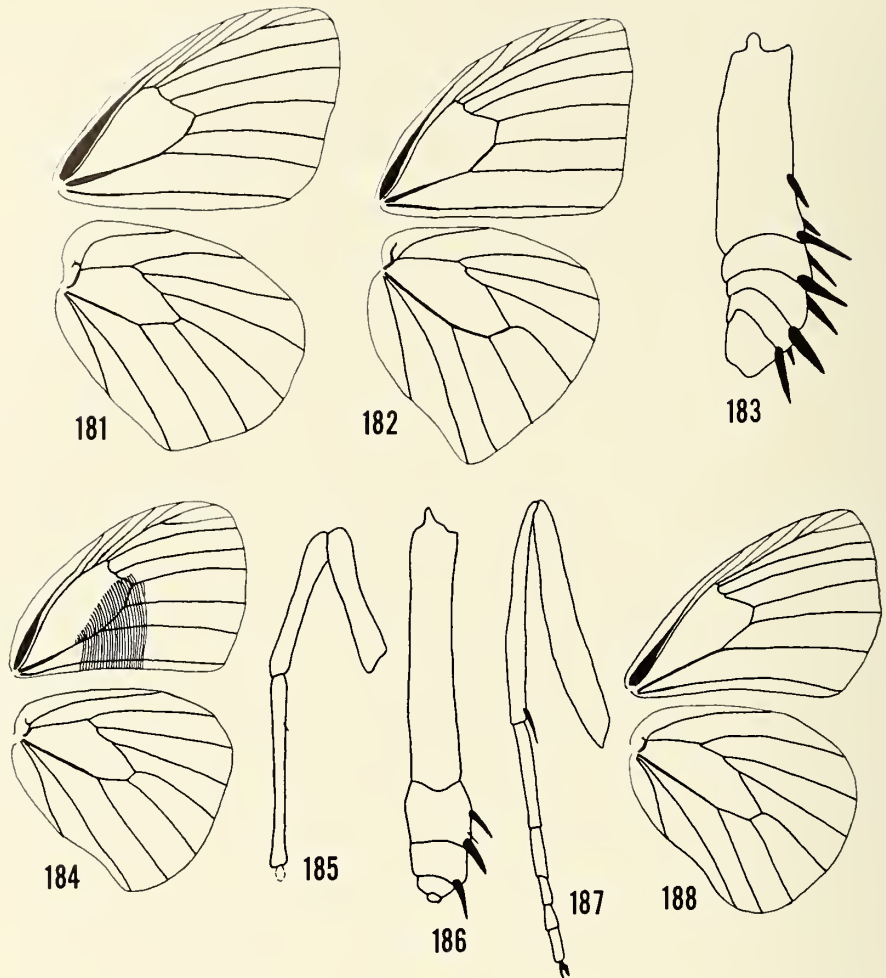
Figs. 181-188. Satyrinae: Ypthimini. 181. *Melampias hyperbius* (Linné), ♂ venation. 182. *Cassionympha cassius* (Godart), ♂ venation. 183. *C. cassius*, ♀ foretarsus. 184. *Callerebia scanda* (Kollar), ♂ venation. 185. *C. scanda*, ♂ foreleg. 186. *C. scanda*, ♀ foretarsus. 187. *C. scanda*, midleg. 188. *Boeberia parmenio* (Boeber), ♂ venation.

Melampias-series

Callyphthima Butler, 1880: 335. Type-species: *Pseudonympha wardii* Butler, by original designation.

Cassionympha van Son, 1955: 96. Type-species: *Satyrus cassius* Godart, by original designation.

Coenyropsis van Son, 1958: 6. Type-species: *Satyrus natalii* Boisduval, by original designation.

Neita van Son, 1955: 101.   Type-speeies: *Pseudonympha neita* Wallengren, by original designation.

Melampias Hübner, [1819](1816-1826): 63.   Type-speeies: *Papilio hyperbius* Linné, designated by Scudder, 1875a: 214.

Neocoenyra Butler, 1885: 758.   Type-species: *Neocoenyra duplex* Butler, by monotypy.

Periplysia Gerstäcker, 1871: 358.   Type-species: *Periplysia leda* Gerstäcker, by monotypy.

Pseudonympha Wallengren, 1857: 31.   Type-speeies: *Papilio hippia* Cramer, designated by Butler, 1868a: 194.

Physcaeneura Wallengren, 1857: 32.   Type-speeies: *Satyrus panda* Boisduval, by monotypy.

Strabena Mabille, 1887: 10, 22.   Type-species: *Satyrus tamatavae* Boisduval, by original designation.

Stygionympha van Son, 1955: 137.   Type-species: *Pseudonympha vigilans* Trimen, by original designation.

Callerebia-series

Argestina Riley, 1922: 469.   Type-speeies: *Callerebia waltoni* Elwes, by original designation.

Boeberia Prout, 1901: 233.   Type-species: *Papilio parmenio* Boeber, by original designation.

> =*Erebomorpha* Elwes, 1899: 351.   Type-species: *Papilio parmenio* Boeber, by original designation.   Preoccupied by *Erebomorpha* Walker, 1860.

Callerebia Butler, 1867e: 217.   Type-speeies: *Erebia scanda* Kollar, by original designation.

Loxerebia Watkins, 1925: 237.   Type-species: *Callerebia pratorum* Oberthür, by original designation.

Paralasa Moore, 1893(1890-1893): 103.   Type-species: *Erebia kalinda* Moore, by original designation.

Genus PALAEONYMPHA Butler, 1871
(Figures 189-195)

Palaeonympha Butler, 1871: 401.   Type-species: *Palaeonympha opalina* Butler, by original designation.

The original description of *Palaeonympha* pointed to its similarity to the North American *Neonympha* (Euptychiini).   If *Palaeonympha* is a member of the Euptychiini it would be the first known Old World representative of that tribe.   It is tempting to place the present genus there, since it is superficially very similar to the American *Megisto cymela* (Cramer), except for the androconial distribution in *opalina*.
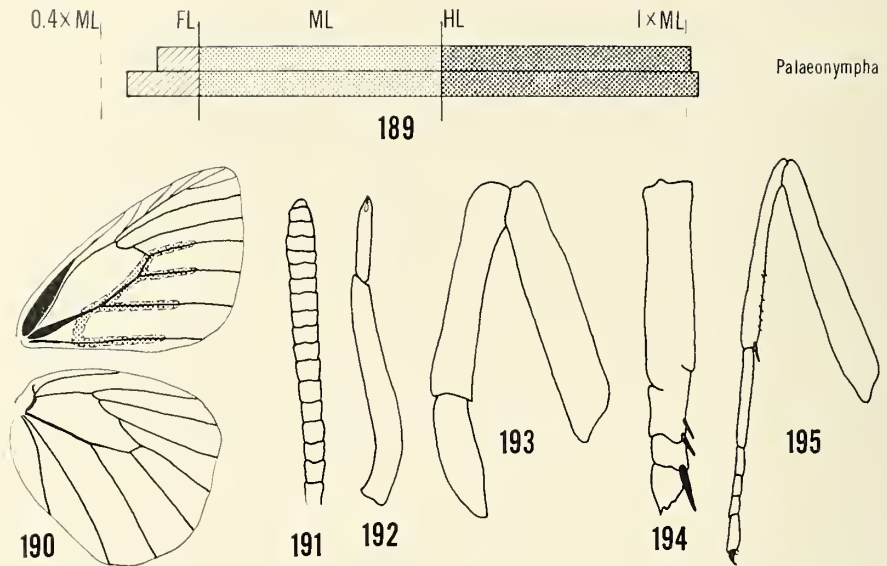
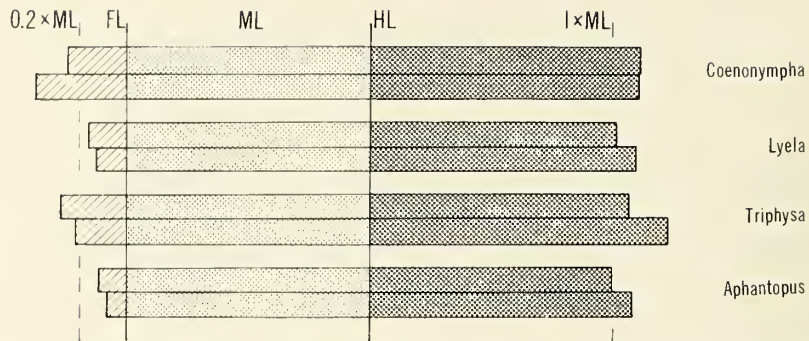Figs. 189-195. Satyrinae: tribe uncertain, *Palaeonympha opalina* Butler. 189. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling). The ML value is unity. The top bar represents the measurements obtained from the male, the bottom bar those from the female. 190. ♂ venation. 191. antennal club. 192. palpus. 193. ♂ foreleg. 194. ♀ foretarsus. 195. midleg.

There are certain similarities between the Euptychiini and the Ypthimini—indeed, they probably arose from the same basic stock—and it is also tempting to place *Palaeonympha* in the latter tribe on purely geographical considerations, but if the present genus is one of the ypthimines, it is the only one with hairy eyes. Certainly *Palaeonympha* is either an ypthimine *or* a euptychiine, or it may represent an intermediate tribe, but I cannot place the genus in either tribe with certainty, and I hesitate to erect a monotypic tribe at this time. *Palaeonympha* is characterized as follows:

The eyes are slightly hairy. The antennae are just less than half as long as the forewing costa. The antennal club is moderately well developed, occupying the distal quarter of the antenna and two and a half to three times as thick as the shaft. The third segment of the palpus is long, about two-fifths the length of the second. The hairs of the second segment of the palpus are three and a half times as long as the segment is wide.

The male foreleg is greatly reduced (Figs. 189, 193): the femur is longer than the tibia, and the tarsus is represented only by a bump at the end of the tibia. The female foreleg is also miniaturized (Figs. 189, 194) with a pentamerous tarsus, the fifth subsegment of which is greatly reduced, bearing spines on the second and third subsegments. The hindlegs are slightly longer than the midlegs (Fig. 189). The midtibia is less than twice the length of the first midtarsal subsegment, smooth dorsad, with no spine at the dorsal, distal end and with well developed tibial spurs.

The forewing cell is very slightly excavate between M_1 and M_2 and about half as long as the forewing costa. The forewing radial veins arise from the cell in a single branch, and Rs and M_1 are separate at their origins. Vein M_2 arises slightly nearer M_1 than M_3, and Cu_1 arises nearer M_3 than Cu_2. Forewing vein Sc and the cubital stem are both much inflated basad, but 2A is not.

The hindwing cell is somewhat produced at the origin of M_3 and is about three-fifths the length of the wing measured to the end of M_3. Hindwing vein $Sc + R_1$ is longer than 3A, and M_3 and Cu_1 are well separated at their origins. Vein M_2 arises nearer M_1 than M_3.

The single species is brown above with a double-pupilled ocellus in M_1-M_2 of the forewing and single-pupilled ones in Rs-M_1 and M_3-Cu_1 of the hindwing. There is an androconial patch of mealy scales along the boundary of the cell and extending out the veins from M_1 to 2A (Fig. 190). The under surface is light brown with discal and extradiscal transverse reddish-brown bands and well developed ocelli as on the upper surface, plus very small ones in forewing spaces M_3-Cu_1 through Cu_2-2A and better developed ones in hindwing spaces M_1-M_2, M_2-M_3 and Cu_2-2A.

Tribe EUPTYCHIINI, new tribe
(Figures 196-210)

This tribe shows the greatest affinities to the Old World Ypthimini and was probably derived from a common stock with it. The euptychiines are less closely related to the Maniolini and Coenonymphini.

The Euptychiini are separable from the Ypthimini on the basis of the slightly longer and more square-cut forewing cell and the ocellus in forewng space M_1-M_3 and differ from the coenonymphines
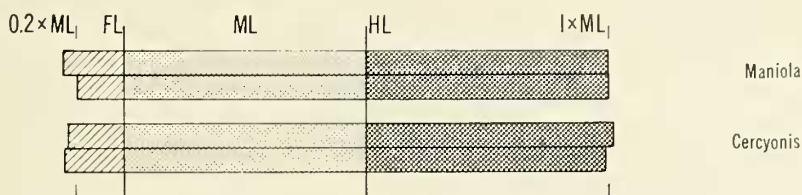
Fig. 196. Satyrinae: Euptychiini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

in that the latter have an excavate forewing cell and a greater abortion of the female foreleg, as well as a greater distention of forewing vein 2A.

All of the genera definitely assigned to the euptychiines are found in the New World, from southern Canada through the Neotropics to temperate South America. Most are woods or forest dwellers, in contrast to most members of the Ypthimini-section. The most comprehensive review of the tribe to date is included in Forster (1964), but, unfortunately, it is by no means complete. The Euptychiini are characterized below.

The eyes are variously naked or hairy. The antennae are short, just under to just over two-fifths the length of the forewing costa. The antennal club is usually weakly developed and about twice the thickness of the shaft (about three times as thick in *Cyllopsis*). The third segment of the palpus is about a third as long as the second segment. The hairs of the second segment of the palpus are variable: in the tropical groups they are about three times as long as the segment is wide, but in the Nearctic *Megisto cymela* (Cramer) the hairs are almost five times the width of the segment.

The male foreleg is reduced, with a monomerous, unspined tarsus; the femur and tibia are of about the same length. The female foreleg
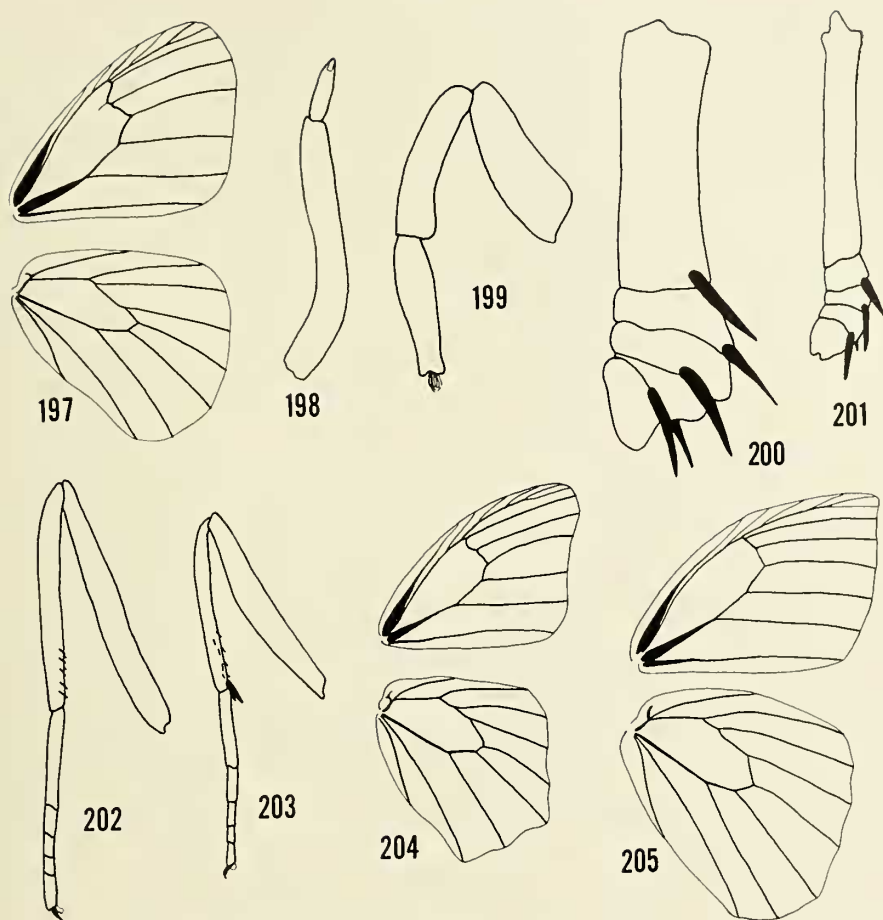
Figs. 197-205. Satyrinae: Euptychiini. 197. *Euptychia mollina* Hübner, ♂ venation. 198. *E. mollina*, palpus. 199. *E. mollina*, ♂ foreleg. 200. *E. mollina*, ♀ foretarsus. 201. *Cissia penelope* (Fabricius), ♀ foretarsus. 202. *E. mollina*, midleg. 203. *Megisto cymela* (Cramer), midleg. 204. *Cyllopsis hedemanni* R. Felder, ♂ venation. 205. *Taygetis mermeria* (Cramer), ♂ venation.

is also reduced, with a pentamerous, clubbed tarsus bearing spines on the second, third and fourth subsegments (also on the first in at least *Neonympha*). The midtibia is one and a half to one and three-quarters times the length of the proximal midtarsal subsegment. The midtibia is variously smooth dorsad in most genera to slightly spiny in such genera as *Neonympha* and spiny in such genera as *Cissia*. The tibial spurs are present and well developed in most species, but

absent in *Euptychia mollina* Hübner, and there is no spine at the dorsal, distal end of the midtibia. The relative lengths of the legs of selected Euptychiini are shown in Fig. 196.

The forewing cell is generally square-cut and varies little from half the length of the forewing costa. The forewing radial veins arise from the cell in two branches (rarely one branch), and veins Rs and M_1 arise well separate. Vein M_2 arises somewhat nearer M_1 than M_3, and Cu_1 arises nearer M_3 than Cu_2. Forewing veins Sc and the cubital stem are basally inflated in all genera, and 2A is inflated in such genera as *Taygetis* and *Oressinoma* (Figs. 205, 210, respectively). The latter genus displays an unusual form of inflation of the veins.

The hindwing cell is straight and produced at the origin of M_3; the cell is half to three-fifths the length of the wing measured to the end of M_3. Hindwing veins $Sc + R_1$ and 3A are of about the same length, M_3 and Cu_1 arising well separate and M_2 arising nearer, occasionally much nearer, M_1 than M_3.

The pattern is reasonably constant. Most species are brown above—they may be white or iridescent purple, blue in part—with or without ocelli. The under surface is usually brown with transverse darker markings and a more or less complete complement of ocelli. *Oressinoma typhla* Westwood is aberrant: white above and below bordered with blackish brown and with reddish lunules in the dark border.

Genera Included in the Euptychiini [1]

[1] Names preceded by asterisks (*) are genera proposed too late for detailed study, but from the original descriptions they are judged to be members of this tribe.

Archeuptychia Forster, 1964: 80. Type-species: *Papilio c'uena* Drury, by original designation.

Caeruleuptychia Forster, 1964: 92. Type-species: *Euptychia caerulea* Butler, by original designation.

Capronnieria Forster, 1964: 73. Type-species: *Euptychia abretia* Capronnier, by original designation.

Cepheuptychia Forster, 1964: 96. Type-species: *Euptychia cephus* Butler, by original designation.

Chloreuptychia Forster, 1964: 119. Type-species: *Papilio chloris* Cramer, by original designation.

Cissia Doubleday, 1848b: 33. Type species: *Papilio clarissa* Cramer (=*Pa*-
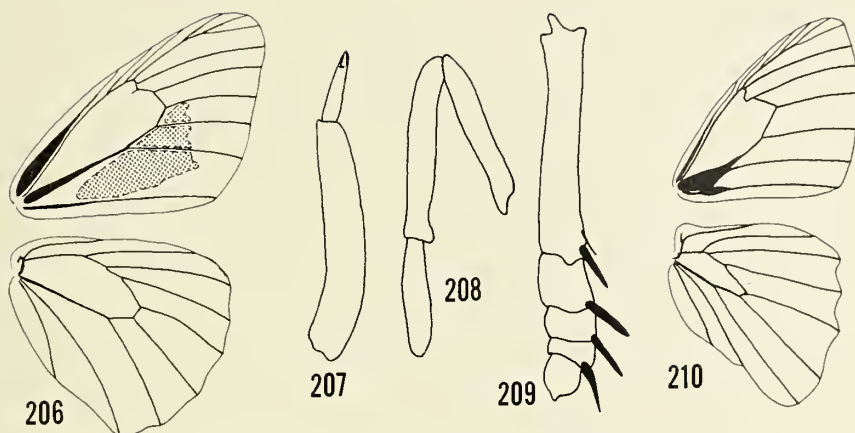
Figs. 206-210. Satyrinae: Euptychiini. 206. *Paramecera xicaque* (Reakirt), ♂ venation. 207. *P. xicaque*, palpus. 208. *P. xicaque,* ♂ foreleg. 209. *P. xicaque,* ♀ foretarsus. 210. *Oressinoma typhla* Westwood, ♂ venation.

pilio penelope Fabricius), by monotypy.

> =*Argyreuptychia* Forster, 1964: 123. Type-species: *Papilio penelope* Fabricius, by original designation.

*Coeruleotaygetis Forster, 1964: 73. Type-species: *Euptychia periboea* Godman and Salvin, by original designation.

Cyllopsis R. Felder, 1869: 474. Type-species: *Cyllopsis hedemanni* R. Felder, by monotypy.

*Erichthodes Forster, 1964: 118. Type-species: *Euptychia erichtho* Butler, by original designation.

Euptychia Hübner, 1818 (1818-1825): 20. Type-species: *Euptychia mollina* Hübner, designated by Hemming, 1937: 150. Butler (1868a: 194) designated *Papilio herse* Cramer as the type, based on *Euptychia* Hübner, [1819](1816-1826): 54, but this designation was invalidated when the appropriate portions of the "Zuträge" were found to be older than those of the "Verzeichniss".

*Euptychoides Forster, 1964: 97. Type species: *Euptychia saturnus* Butler, by original designation.

*Godartiana Forster, 1964: 118. Type-species: *Satyrus byses* Godart, by original designation.

*Harjesia Forster, 1964: 78. Type-species: *Taygetis blanda* Möschler, by original designation.

*Haywardina Forster, 1964: 109. Type-species: *Satyrus necys* Godart, by original designation. Preoccupied by *Haywardina* Aczél, 1952, but no replacement name is proposed.

*Hermeuptychia Forster, 1964: 87. Type-species: *Papilio hermes* Fabricius, by original designation.

Magneuptychia Forster, 1964: 125. Type-species: *Papilio libye* Linné, by
     original designation.
Megeuptychia Forster, 1964: 122. Type-species: *Nymphalis autonoe* Cramer,
     by original designation.
Megisto Hübner, [1819](1816-1826): 54. Type-species: *Papilio eurytus* Fa-
     bricius (=*Papilio cymela* Cramer), designated by Butler, 1868b: 14.
Moneuptychia Forster, 1964: 92. Type-species: *Euptychia soter* Butler, by
     original designation.
Neonympha Hübner, 1818(1818-1825): 8. Type-species: *Papilio areolatus*
     Smith and Abbot, designated by Hemming, 1937: 150.
Oressinoma Westwood, 1852, *in* Doubleday, Westwood and Hewitson, 1846-
     1852: 371. Type-species: *Oressinoma typhla* Westwood, by monotypy.
          =*Ocalis* Westwood, 1852, *in* Doubleday, Westwood and Hewitson,
               1846-1852: 371. Type-species: *Oressinoma typhla* Westwood, by
               monotypy. Listed in synonymy of *Oressinoma* Westwood.
Paramecera Butler, 1868b: 98. Type-species: *Neonympha xicaque* Reakirt,
     by monotypy.
Parataygetis Forster, 1964: 79. Type-species: *Taygetis albinotata* Butler, by
     original designation.
Pareuptychia Forster, 1964: 83. Type-species: *Papilio hesione* Sulzer, by
     original designation.
Parypththimoides Forster, 1964: 106. Type-species: *Neonympha poltys*
     Prittwitz, by original designation.
Pharneuptychia Forster, 1964: 91. Type-species: *Satyrus phares* Godart, by
     original designation.
Pindis R. Felder, 1869: 475. Type-species: *Pindis squamistriga* R. Felder, by
     monotypy.
Posteuptychia Forster, 1964: 137. Type-species: *Euptychia mycalesoides*
     Felder, by original designation.
Posttaygetis Forster, 1964: 74. Type-species: *Papilio penelea* Cramer, by
     original designation.
Praefaunula Forster, 1964: 137. Type-species: *Euptychia armilla* Butler, by
     original designation.
Pseudeuptychia Forster, 1964: 86. Type-species: *Euptychia languida* Butler,
     by original designation.
Pseudodebis Forster, 1964: 75. Type-species: *Papilio valentina* Cramer,
     by original designation.
Rareuptychia Forster, 1964: 87. Type-species: *Euptychia clio* Weymer, by
     original designation.
Satyrotaygetis Forster, 1964: 73. Type-species: *Euptychia satyrina* Bates,
     by original designation.
Splendeuptychia Forster, 1964: 128. Type-species: *Euptychia ashna* Hew-
     itson, by original designation.
Taygetina Forster, 1964: 77. Type-species: *Taygetis banghaasi* Weymer, by
     original designation.

Taygetis Hübner, [1819](1816-1826): 55.   Type-species: *Papilio mermeria*
    Cramer, designated by Westwood, 1852, *in* Doubleday, Westwood and
    Hewitson, 1846-1852: 355.   Hemming (in press) accepts the designa-
    tion of *Papilio virgilia* Cramer as the type-species by Butler, 1868a: 194,
    but the intent of Westwood to designate *mermeria* as the type-species
    is unmistakable.
*Vareuptychia Forster, 1964: 125.   Type-species: *Euptychia similis* Butler,
    by original designation.
*Weymerana Forster, 1964: 108.   Type-species: *Euptychia viridicans* Wey-
    mer, by original designation.
*Ypthimoides Forster, 1964: 100.   Type-species: *Neonympha yphthima* Felder,
    by original designation.
*Zischkaia Forster, 1964: 116.   Type-species: *Euptychia fumata* Butler, by
    original designation.

Tribe COENONYMPHINI, new tribe
(Figures 211-222)

The Coenonymphini are intimately related to the ypthimines
and probably replace them in the north temperate zone savannas of
both hemispheres.   There are some relationships suggested with the
maniolines, the latter group occupying scrub country environments:
probably both evolved from a basic ypthimine stock.   There is little
to connect the coenonymphines with the Euptychiini or the Erebiini,
two isolated tribes of the Ypthimini-section.

The excavate forewing cell serves to distinguish most coeno-
nymphines from most ypthimines, and the very long midtibia (over
twice as long as the first midtarsal segment in all genera but *Aphan-
topus*) is unique in the Ypthimini-section.   The female foreleg of the
Ypthimini and the Euptychiini is fully formed, having five tarsal sub-
segments, whereas that of the Coenonymphini is lacking at least one
of the subsegments.

The Coenonymphini are exclusively Holarctic and are grassland
species.   Almost all are temperate, few (*e. g., Coenonympha mix-
turata* Alpheraky) being found so far north as the subarctic.   The
Coenonymphini are characterized as follows:

The eyes are naked.   The antennae are always shorter than half
the length of the forewing costa, and those of *Lyela* and *Triphysa*
are less than two-fifths the length of the forewing.   The antennal club
is variable in its development: in *Aphantopus* the club is only about

Fig. 211. Satyrinae: Coenonymphini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

two and a half times as thick as the shaft, five times as thick in *Triphysa* (Fig. 220) and seven times the thickness of the shaft in *Lyela*. The third segment of the palpus is generally half to one-third as long as the second, but the third segment is less than one-sixth the length of the second in *Triphysa* and *Lyela*. The hairs of the second segment of the palpus are about four times as long as the segment is wide.

The male foreleg is weakly developed with a monomerous, unspined (weakly spined in *Lyela*) tarsus. The forefemur and foretibia are of about the same length; in some genera slight variations may be apparent. The female foreleg is reduced and is of two general types: in such genera as *Coenonympha* there are four tarsal subsegments which are spined on at least the third and fourth ones, whereas in other genera like *Chortobius*, *Lyela* and *Triphysa* there is but one, unspined tarsal subsegment. With the exception of *Aphantopus*, the midtibia is very long, greater than twice as long as the first midtarsal subsegment. The tibial spurs are present and well developed in all genera but *Triphysa*, in which they are totally absent. The midtibia is smooth dorsad and has no spine at the dorsal, distal end. The hindlegs are significantly longer than the midlegs (Fig. 211).

The forewing cell is deeply excavate and varies little from half the length of the forewing costa. The forewing radial veins generally arise in two branches from the cell, but in three branches in *Aphan-*

topus; veins Rs and M_1 are separate at their origins, although they may be approximate. Vein M_2 arises nearer M_1 than M_3, and Cu_1 arises midway between M_3 and Cu_2, or slightly nearer M_3. Fore-
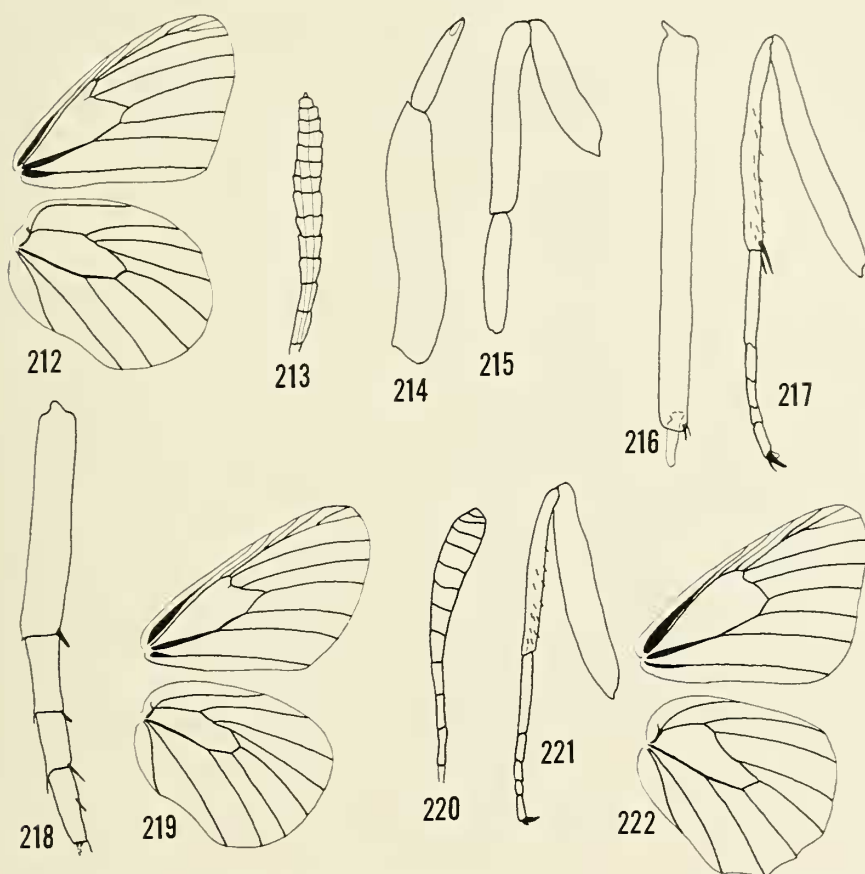
Figs. 212-222. Satyrinae: Coenonymphini. 212. *Coenonympha oedippus* (Fabricius), ♂ venation. 213. *C. oedippus,* antennal club. 214. *C. oedippus,* palpus. 215. *C. oedippus,* ♂ foreleg. 216. *Chortobius pamphilus* (Fabricius), ♀ foretarsus. 217. *C. oedippus,* midleg. 218. *C. oedippus,* ♀ foretarsus. 219. *Triphysa phryne* (Pallas), ♂ venation. 220. *T. phryne,* antennal club. 221. *T. phryne,* midleg. 222. *Aphantopus hyperantus* (Linné), ♂ venation.

wing veins Sc, the cubital stem and 2A are all inflated, though the latter may be only slightly thickened.

The hindwing cell is square-cut distad and half to three-fifths the length of the wing to the end of M_3. Hindwing vein $Sc + R_1$ is

as long as, or longer than, 3A. Veins M_3 and Cu_1 are separate,
but close together, at their origins, and M_2 arises nearer, or much
nearer, M_1 than M_3.

The pattern is fairly constant. The upper surface is brown to
tawny with few, if any, ocelli. The under surface of the forewings
is likewise brown to tawny, and the hindwings are brown to grayish-
olive, often with a light mesial band, with a more or less developed
series of ocelli on both wings. *Triphysa phryne* (Pallas) is the only
species to show marked sexual dimorphism: the male is brown with
a more complete set of ocelli than is usual in the tribe, and the female
is white with a full complement of ocelli.

Genera Included in the Coenonymphini

Aphantopus Wallengren, 1853: 30. Type-species: *Papilio hyperantus* (mis-
      spelled "*hyperanthus*") Linné, by monotypy.
Chortobius [Dunning and Pickard], 1858: 5. Type-species: *Papilio pamphilus*
      Linné, designated by Moore, 1893 (1890-1893): 51-52.
Coenonympha Hübner, [1819](1816-1826): 65. Type-species: *Coenonympha*
      oedipe Hübner (=*Papilio oedippus* Fabricius), designated by Butler,
      1868a: 194 (as *Papilio geticus* Esper).
Dubierebia Muschamp, 1915b: 20. Type-species: *Coenonympha myops*
      Staudinger, by original designation.
Lyela Swinhoe, 1908: 60. Type-species: *Lyela macmahoni* Swinhoe, by origi-
      nal designation.
Sicca Verity, 1953: 83. Type-species: *Papilio dorus* Esper, by original desig-
      nation. Proposed as a subgenus of *Coenonympha* Hübner.
Triphysa Zeller, 1850: 308. Type-species: *Papilio tircis* Stoll (=*Papilio*
      phryne Pallas), designated by Butler, 1868a: 194.
         =*Phryne* Herrich-Schäffer, 1844 (1843-1856): 90. Type-species:
         Papilio tircis Stoll (=*Papilio phryne* Pallas), by monotypy. Pre-
         occupied by *Phryne* Meigen, 1800.

Tribe MANIOLINI Hampson, 1918
(Figures 223-232)

Maniolinae Hampson, 1918: 385; Maniolidi Verity, 1953: 228, 237.

This tribe is most closely related to the Coenonymphini; probably
both tribes evolved in the Holarctic from a basic ypthimine stock.
The maniolines are much more distantly related to either the Eupty-
chiini or the Erebiini.

The maniolines are distinguished from other members of the

Ypthimini-section by forewing vein M_2 arising midway between M_1 and M_3 (in other tribes M_2 arises nearer M_1), and by the distribution of androconia. Whereas the Euptychiini and the Ypthimini
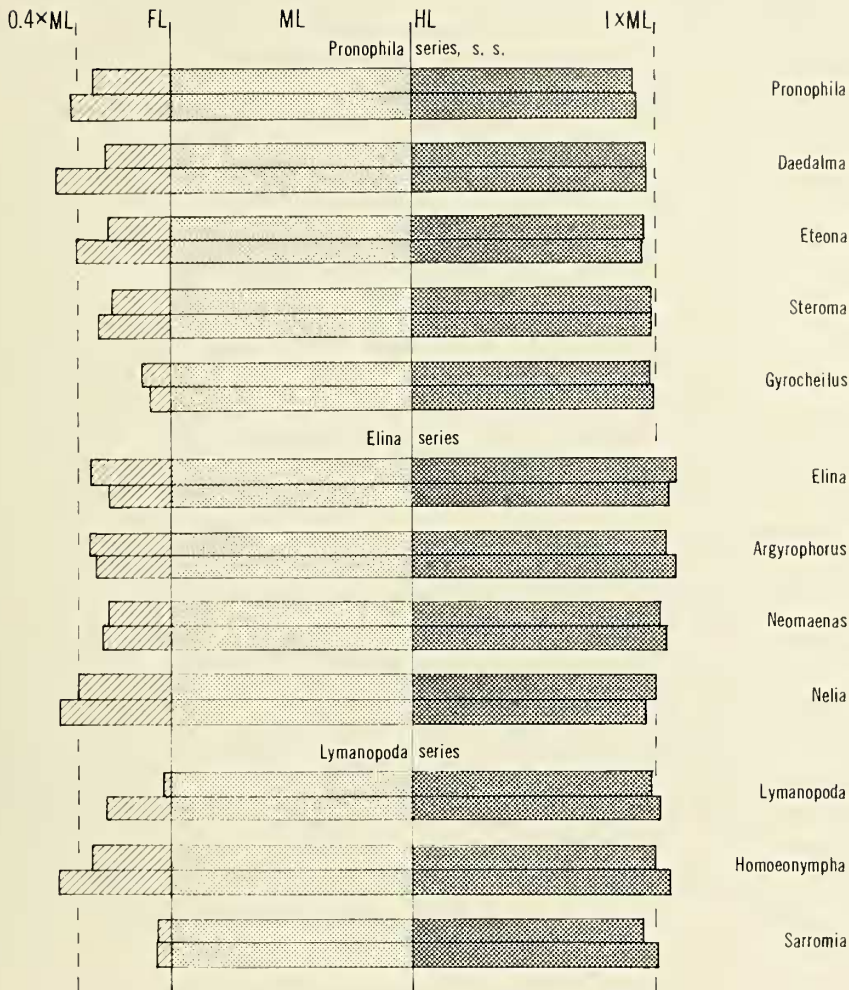

Fig. 223. Satyrinae: Maniolini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

have a pentamerous female foreleg, this tribe shows leg abortion in all genera, like the Coenonymphini.

Cercyonis is considered by many authors (*e.g.,* Hemming, in press) to be biologically synonymous with *Minois* Hübner. The latter genus, however, is a member of the Satyrini, as shown by the production of the hindwing cell along vein M_2 and the typically satyrine configuration of the midleg (Fig. 301). The midleg of *Cercyonis* is typical of the Maniolini (Fig. 228) and has nothing in common evolutionarily with *Minois*. The proper assignment of *Cercyonis* again demonstrates the necessity of looking beyond mere superficial similarities.

The maniolines are found throughout the north temperate zone, and a few members are also found in the Arctic. These butterflies seem to replace the grassland Coenonymphini in scrublands. The Maniolini are characterized as follows:

The eyes are naked. The antennae are greater than two-fifths, but less than half, the length of the forewing costa. The antennal club is weakly developed, from less than twice to about two and a half times the thickness of the shaft, and occupying the distal third to a quarter of the antenna. The third segment of the palpus is about one-third of the length of the second. The hairs of the second segment of the palpus are long, about four to five times as long as the segment is thick.

The male foreleg is greatly reduced, the femur and the tibia are

of approximately the same length and the tarsus is monomerous and unspined. The female foreleg is also greatly reduced with a mono- or dimerous tarsus without spines. The mid- and hindlegs are of
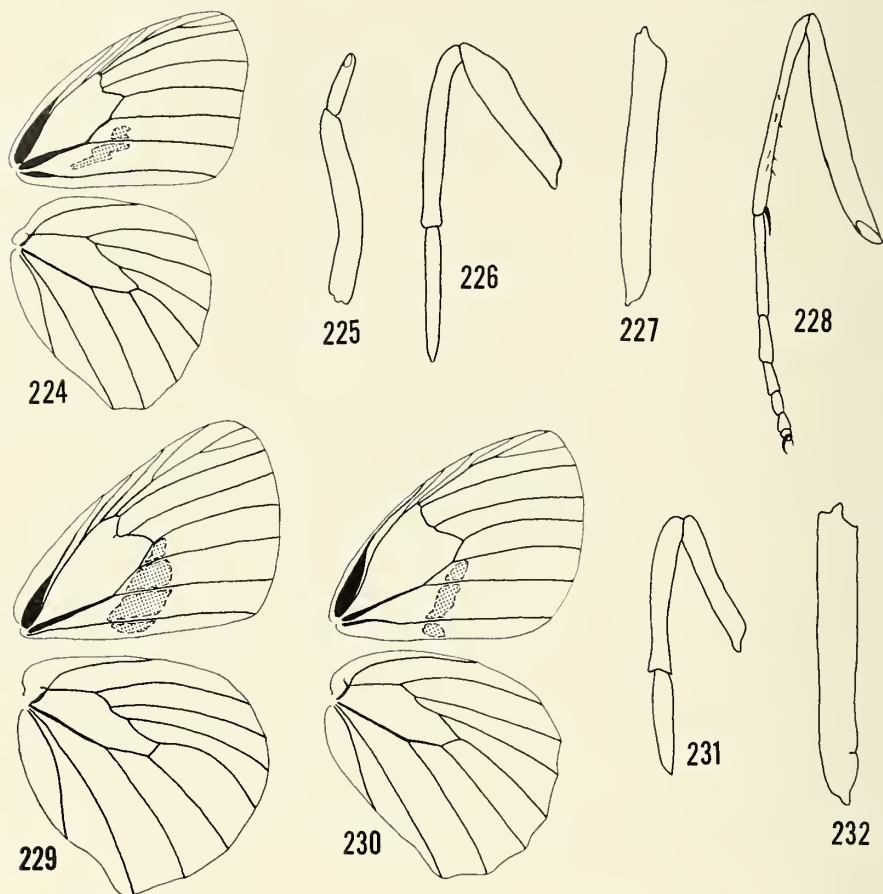
Figs. 224-232. Satyrinae: Maniolini. 224. *Maniola jurtina* (Linné), ♂ venation. 225. *M. jurtina*, palpus. 226. *M. jurtina*, ♂ foreleg. 227. *M. jurtina*, ♀ foretarsus. 228. *M. jurtina*, midleg. 229. *Pyronia tithonus* (Linné), ♂ venation. 230. *Cercyonis pegala* (Fabricius), ♂ venation. 231. *C. pegala*, ♂ foreleg. 232. *C. pegala*, ♀ foretarsus.

about the same length (Fig. 223). The midtibia is somewhat less than twice as long as the basal midtarsal subsegment, without spines dorsad or at the dorsal distal end and with well developed tibial spurs.

The forewing cell is somewhat excavate and rather uniformly half

as long as the forewing costa. The forewing radial veins arise in three branches from the cell, and veins Rs and M_1 are separate at their origins. Vein M_2 arises about midway between M_1 and M_3, and Cu_1 arises nearer M_3 than Cu_2. Forewing vein Sc is always inflated basally; the cubital stem and 2A may be greatly inflated (*Maniola*, Fig. 224) or not noticeably inflated (*Cercyonis*, Fig. 230).

The hindwing cell is produced at the origin of M_3 and varies from less than half to as long as three-fifths the length of the wing measured to the end of M_3. Vein $Sc + R_1$ is longer than 3A, and M_3 and Cu_1 are well separated at their origins. Vein M_2 arises nearer M_1 than M_3.

The upper surface is either tawny with brown margins or brown with or without a yellow discal patch on the forewing with the ocelli, if they are present, in the forewing spaces M_1-M_3 and Cu_2-2A and on the hindwing at the tornus. Beneath the wings are light brown with darker brown striae and moderately well developed ocelli on both wings.

Genera Included in the Maniolini

Cercyonis Scudder, 1875b: 241. Type-species: *Papilio alope* Fabricius (= *Papilio pegala* Fabricius), by original designation.

Hyponephele Muschamp, 1915a: 156. Type-species: *Papilio lycaon* Rottemburg, by monotypy.

Idata deLesse, 1952: 72. Type-species: *Pyronia cecilia* Vallantin, by original designation. Proposed as a subgenus of *Pyronia* Hübner.

Maniola Schrank, 1801: 152. Type-species: *Maniola lemur* Schrank (=*Papilio jurtina* Linné), designated by Scudder, 1875a: 211.

> =*Epinephele* Hübner, [1819](1816-1826): 59. Type-species: *Papilio janira* Linné (=*Papilio jurtina* Linné), designated by Butler, 1868a: 194. Note that many authors have misspelled this name as "*Epinephile*" or "*Epinephila*".

Pasiphana de Lesse, 1952: 72. Type-species: *Hipparchia bathseba* Fabricius, by original designation. Proposed as a subgenus of *Pyronia* Hübner.

Pyronia Hübner, [1819](1816-1826): 59. Type-species: *Pyronia tithone* Hübner (=*Papilio tithonus* Linné), designated by Scudder, 1875a: 261.

Tribe EREBIINI Tutt, 1896
(Figures 233-246)

Erebiinae Tutt, 1896: 87, 402.

This tribe shows certain affinities with the Ypthimini and to the Satyrini-section, but is closer to the former; the similarity to the latter

is probably convergence. Structurally no group is exceptionally close
to the erebiines, except the *Callerebia*-series of the Ypthimini.
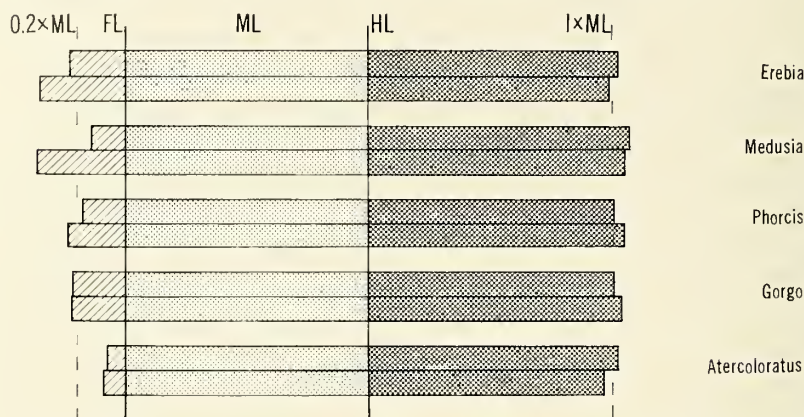
Fig. 233. Satyrinae: Erebiini. Relative lengths of the femur + tibia
+ tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and
hindlegs (HL, heavy stippling) of selected genera. In all instances the ML
value is unity. The top bar for each genus represents the measurements
obtained from males, the bottom bar those from females.

The erebiines may be distinguished from other satyrines of the
Ypthimini-section by the extremely short third palpal segment, which
is less than a fourth as long as the second segment in all genera. The
facies of the species are characteristic, but, as indicated in the dis-
cussions of the Dirini, the Hypocystini and the Pronophilini, some
other genera outside the present tribe share the dark coloration,
rounded wings and alpine habits with these butterflies. The very
slight inflation of the forewing veins, even of Sc, is atypical of the
Ypthimini-section.

All of the erebiines are Holarctic, and many species are found
in the high Arctic, as well as in alpine situations; few are at home in
truly temperate climates. Warren (1936) has admirably mono-
graphed this group. The Erebiini are characterized as follows:

The eyes are naked. The antennae are from just over two-fifths
to greater than half the length of the forewing costa. The antennal
club is moderately well to very well developed, generally occupying
the distal quarter of the antenna and inflated as much as five times
the thickness of the shaft. The third segment of the palpus is very
short, from one-quarter to one-sixth the length of the second. The
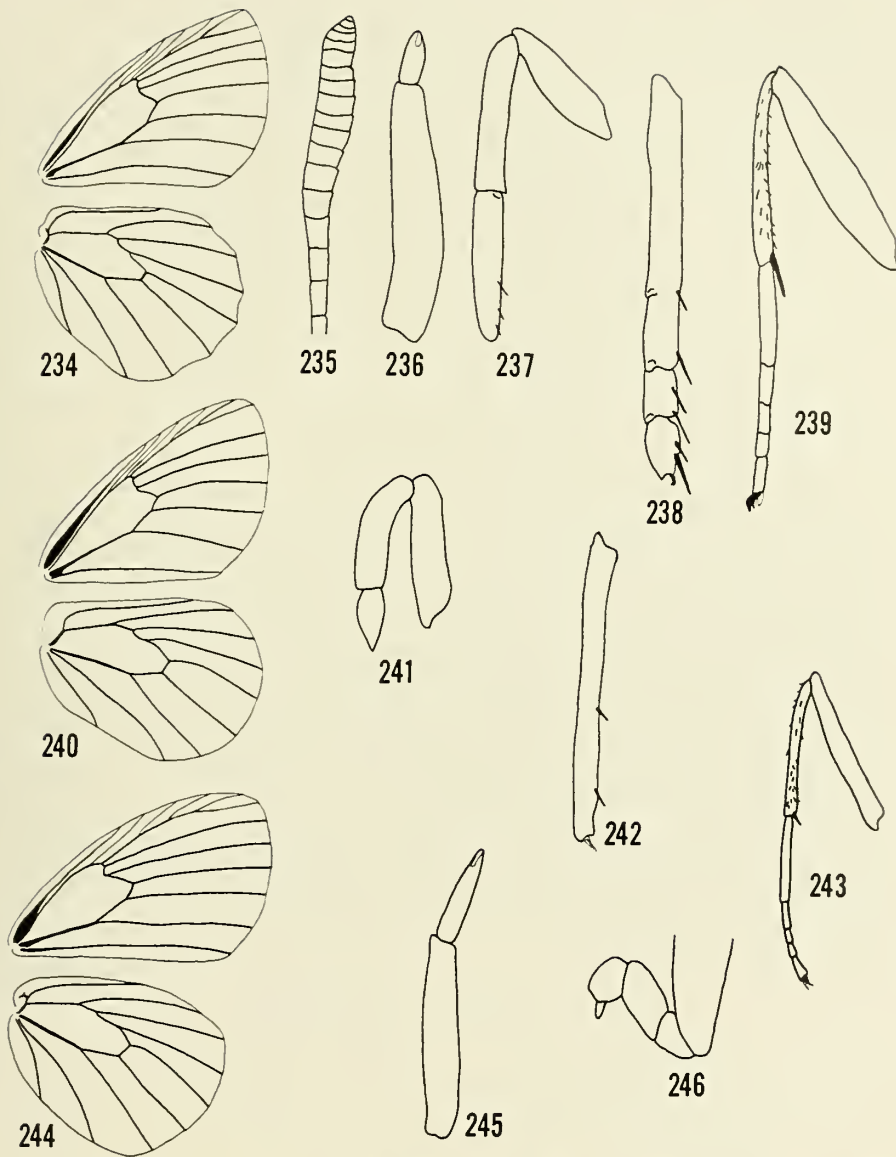
Figs. 234-246. Satyrinae: Erebiini. 234. *Erebia ligea* (Linné). ♂ vena-
tion. 235. *E. ligea*, antennal club. 236. *E. ligea*, palpus. 237. *E. ligea*, ♂
foreleg. 238. *E. ligea*, ♀ foretarsus. 239. *E. ligea*, midleg. 240. *Phorcis
epistygne* Hübner, ♂ venation. 241. *P. epistygne*, ♂ foreleg. 242. *P. epi-
stygne*, ♀ foretarsus. 243. *P. epistygne*, midleg. 244. *Atercoloratus alini*
(Bang-Haas), ♂ venation. 245. *A. alini*, palpus. 246. *A. alini*, ♂ foreleg, in-
cluding trochanter and distal portion of coxa.

hairs on the second segment of the palpus are long, between three and five times as long as the segment is wide.

The male foreleg is reduced with a mono- or dimerous, unspined or weakly spined tarsus; the femur is generally as long as, or longer than, the tibia. The development of the female foreleg is variable, though the leg itself is always greatly miniaturized (Fig. 233). There are two to five tarsal subsegments with spines on all but the last one. The midleg is about as long as, and frequently longer than, the hindleg (Fig. 233). The midtibia is from just under to well over one and a half times the length of the first midtarsal sub-segment. The midtibia never bears a spine at its dorsal, distal end and is usually smooth dorsad, but slightly spiny in *Phorcis* (Fig. 243). The tibial spurs are present and well developed.

The forewing cell is slightly excavate and varies little from half the length of the forewing costa. The forewing radial veins arise in three branches from the cell, and veins Rs and M_1 are well separated at their origins. Vein M_2 arises much nearer M_1 than M_3, and Cu_1 arises nearer M_3 than Cu_2. Forewing vein Sc is always more or less inflated, the cubital stem is somewhat inflated and 2A hardly at all.

The hindwing cell is produced at the origin of M_3 and is half to three-fifths as long as the wing measured to the end of M_3. Vein $Sc + R_1$ is longer than 3A, and M_3 and Cu_1 are well separated at their origins. Vein M_2 arises nearer M_1 than M_3.

These are dark insects with very little pattern on either surface except scattered ocelli and a forewing tawny to russet shade; either or both pattern features may be absent. Illustrations of the species are given by Warren (1936).

Genera Included in the Erebiini

Atercoloratus Bang-Haas, 1938: 178. Type-species: *Coenonympha alini* Bang-Haas, by original designation.

Erebia Dalman, 1816: 58. Type-species: *Papilio ligea* Linné, by original designation.
> =*Epigea* Hübner, [1819](1816-1826): 62. Type-species: *Papilio ligea* Linné, designated by Hemming, 1933: 198.

Gorgo Hübner, [1819](1816-1826): 64. Type-species: *Papilio ceto* Hübner, designated by Hemming, 1933: 198.

Marica Hübner, [1819](1816-1826): 63. Type-species: *Papilio stygne* Ochsenheimer, designated by Hemming, 1933: 198.

Medusia Verity, 1953: 179. Type-species: *Papilio medus* Schiffermiller, by original designation. Proposed as a subgenus of *Erebia* Dalman.

Oreina Westwood, 1841: 76. Type-species: *Papilio cassiope* Fabricius, designated by Butler, 1868a: 194.

Phorcis Hübner, [1819](1816-1826): 62. Type-species: *Phorcis epistygne* Hübner, designated by Hemming, 1933: 198.

Simplica Verity, 1953: 194. Type-species: *Papilio epiphron* Knoch, by original designation. Proposed as a subgenus of *Erebia* Dalman.

Syngea Hübner, [1819](1816-1826): 62. Type-species: *Papilio pronoe* Esper, designated by Hemming, 1933: 198.

Triariia Verity, 1953: 186. Type-species: *Papilio triarius* de Prunner, by original designation. Proposed as a subgenus of *Erebia* Dalman.

Truncaefalcia Verity, 1953: 188. Type-species: *Papilio aethiops* Esper, by originial designation. Proposed as a subgenus of *Erebia* Dalman.

Tribe DIRINI, new tribe
(Figures 247-259)

This tribe is not as primitive as the hypocystines, as may be seen form examination of the forelegs of both sexes, even though it seems to connect the remainder of the Satyrini-section with the South African members of the Lethini—a convergence which is probably ecological and with little phylogenetic significance. The forelegs of both sexes are greatly reduced, about as much so as in any tribe; the dirines are nevertheless primitive members of the Satyrini-section. There is little to connect the Dirini—or any member of the Satyrini-section, for that matter—with the Hypocystini except the configuration of the hindwing cell (Figs. 248, 254, 257). In common with the Satyrini, Pronophilini (usually to a lesser extent) and Melanargiini are the greatly reduced forelegs, the spiny midtibiae and the well developed tibial spurs of the present tribe. Some species have a well developed dorsal, distal spine at the end of the midtibia (Fig. 259), a characteristic shared with the Satyrini and indicating a close relationship between these two tribes.

The Dirini are characterized chiefly by the short forewing cell, always less than half the length of the wing; in other Satyrinae the cell is half the length of the wing or greater. The forewing cell is also rounded and reminiscent of that of the Lethini.

All members of this tribe are restricted to South Africa and are well illustrated by van Son (1955). The Dirini are characterized as follows:

The eyes are hairy in all genera. The antennae are approximately two-fifths the length of the forewing costa. The antennal club is
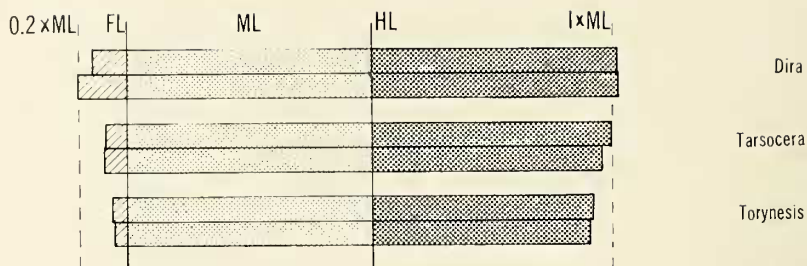
Fig. 247. Satyrinae: Dirini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

abrupt, occupying the distal one-fifth to one-third of the antenna and three to five times as thick as the shaft (Fig. 249). The third segment of the palpus is usually about a third the length of the second, but is half as long in *Cassus* (Fig. 254) and only one-ninth as long in *Torynesis* (Fig. 257). The hairs of the second palpal segment are two or three times as long as the segment is wide.

The male foreleg is greatly reduced (Fig. 247), particularly as regards the tibia and tarsus. The femur is always more than twice as long as the tibia, and the tarsus has one or two unspined subsegments (Figs. 251, 258). The female foreleg is also greatly reduced, frequently as much so as that of the male, with a mono- or dimerous, unspined tarsus (Fig. 252). The midleg is as long as, and occasionally much longer than (*Torynesis*), the hindleg (Fig. 247). The midtibia is almost twice as long as the first midtarsal subsegment in some genera such as *Dira* (Fig. 253), but in *Torynesis* (Fig. 259) and *Dingana* the midtibia is only slightly longer than is the proximal midtarsal subsegment. The midtibia is spiny dorsad and bears well developed tibial spurs; in most genera there is no spine at the dorsal, distal end of the midtibia, but the spine is weakly developed in *Dingana*. The configuration of the midleg in *Dingana* and *Torynesis* strongly suggests that of the Satyrini.

The forewing cell is generally rounded distad and is greater than two-fifths, but less than half, the length of the forewing costa. The forewing radial veins arise from the cell in three branches, and Rs and M_1 are well separated at their origins. Vein M_2 arises nearer M_1 than M_3, and Cu_1 arises nearer M_3 than Cu_2. Only forewing vein
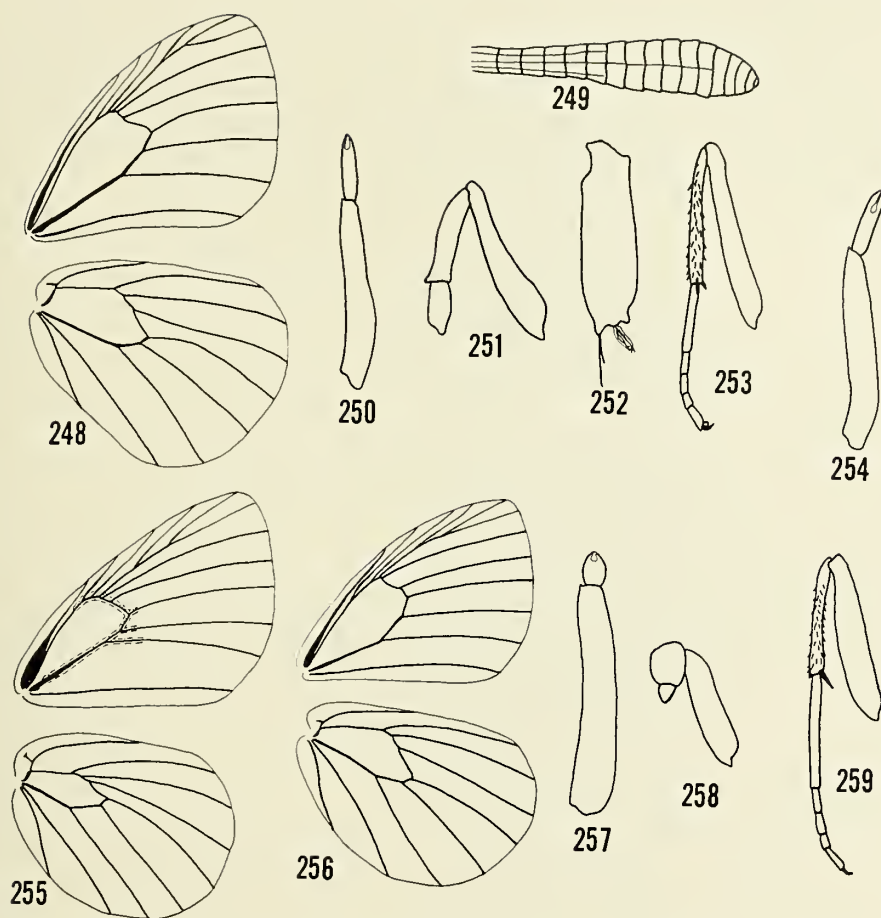
Figs. 248-259. Satyrinae: Dirini. 248. *Dira clytus* (Linné), ♂ venation. 249. *D. clytus*, antennal club. 250. *D. clytus*, palpus. 251. *D. clytus*, ♂ foreleg. 252. *D. clytus*, ♀ foretarsus. 253. *D. clytus*, midleg. 254. *Cassus cassus* (Linné), palpus. 255. *C. cassus*, ♂ venation. 256. *Torynesis mintha* (Geyer), ♂ venation. 257. *T. mintha*, palpus. 258. *T. mintha*, ♂ foreleg. 259. *T. mintha*, midleg.

Sc is inflated basad, and it is only slightly thickened.

The hindwing cell is somewhat produced at the origin of M_3 and about half the length of the wing measured to the end of M_3. Hindwing veins $Sc + R_1$ and 3A are of about the same length, and veins M_3 and Cu_1 arise separately, though they may be approximate. Vein M_2 arises much nearer M_1 than M_3.

These butterflies are dark colored insects on the upper surface with ocelli in forewing spaces M_1-M_3 and Cu_2-2A. On the under surface the forewing ocelli are repeated and the hindwings are patterned by pale mottling and veinal markings. The general aspect is that of the Erebiini or the Satyrini. The species are figured by van Son (1955).

Genera Included in the Dirini

Cassus van Son, 1955: 79. Type-species: *Papilio cassus* Linné, by original designation.

Dingana van Son, 1955: 70. Type-species: *Leptoneura dingana* Trimen, by original designation.

Dira Hübner, [1819](1816-1826): 60. Type-species: *Dira clyte* Hübner (= *Papilio clytus* Linné), designated by Scudder, 1875a: 157.
> =*Leptoneura* Wallengren, 1857: 31. Type-species: *Papilio clytus* Linné, by monotypy.

Tarsocera Butler, 1899: 903. Type-species: *Leptoneura cassina* Butler, by monotypy.

Torynesis Butler, 1899: 903. Type-species: *Dira mintha* Geyer, by monotypy.
> =*Mintha* van Son, 1955: 76. Type-species: *Dira mintha* Geyer, by original designation.

Tribe PRONOPHILINI Clark, 1947
(Figures 260-294)
Pronophilinae Clark, 1947: 149.

This tribe was derived from a basic Satyrini-like stock of Old World origin but is more primitive than any present-day Satyrini, particularly as regards the forelegs, hence the pronophilines are placed before the satyrines in this discussion. In addition to the affinity with the Satyrini, the Pronophilini share some characteristics (though not particularly important ones) with the South African Dirini, which are, in turn, the most primitive tribe within the Satyrini-section. The pronophilines are only very distantly related to the *Xenica*-series of the Hypocystini; hence, any trans-Antarctic distribution of the family is doubtful.

As in the Hypocystini and Dirini, convergent evolution toward the Holarctic *Erebia* is shown by several high-altitude pronophilines of the *Lymanopoda*-series. Several members of the *Elina*-series of the present tribe show resemblance to members of the Holarctic
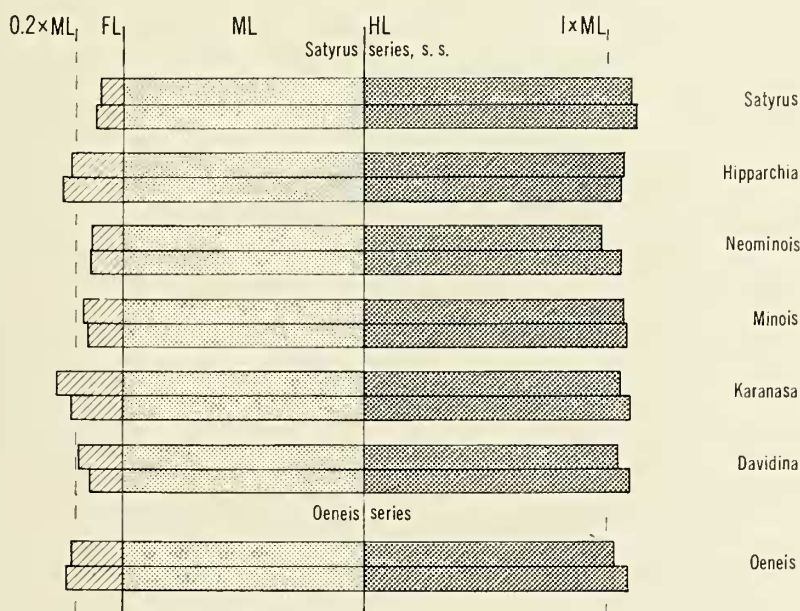
Fig. 260.   Satyrinae: Pronophilini.   Relative lengths of the femur +
tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stip-
pling) and hindlegs (HL, heavy stippling) of selected genera.   In all instances
the ML value is unity.   The top bar for each genus represents the measure-
ments obtained from males, the bottom bar those from females.

Maniolini; indeed, they were long considered members of *Maniola*
(= *Epinephele*), but on structural grounds these butterflies are per-
fectly valid pronophilines.   Many aberrant patterns have evolved in
the great adaptive radiation of this tribe in the Neotropics: the Chilean

species *Argyrophorous argenteus* Blanchard is silver above, while *Lymanopoda samius* Westwood is caerulean blue on the upper surface and members of *Drucina* resemble nymphalids or danaids more than they do other satyrids.

The Pronophilini are the only Neotropical satyrids which have the hindwing crossvein m_1-m_2 produced distad at M_2 *and* hindwing vein $Sc + R_1$ completely fused throughout its entire length. The present tribe can be distinguished from the Satyrini by the longer midtibia—never less than one and a half times the length of the first midtarsal subsegment—and the lack of a dorsal, distal midtibial spine. The more aborted forelegs serve to distinguish these butterflies from the Hypocystini.

All members of the Pronophilini are Neotropical with the exception of a single genus (*Gyrocheilus*) which penetrates the southernmost Nearctic. Many genera, particularly those of the *Elina*-series, are found in the temperate parts of South America. Three groups are recognized within the pronophilines:

The *Pronophila*-series, *sensu stricto,* characterized by the generally broad wings and rounded margins of the hindwings, except where modified by tails. The vast majority of these butterflies are found in tropical forests.

The *Elina*-series, characterized by broad wings, but the hindwings are usually produced in the anal region. The forelegs are more reduced than in the *Pronophila*-series. Most of these butterflies are found in the South Temperate region.

The *Lymanopoda*-series, characterized by the narrow wings, rounded hindwing margins and reduced forelegs. Most of these species are found in the Andean highlands.

The Pronophilini are characterized as follows:

The eyes are usually hairy, but are naked in such diverse genera as *Argyrophorus, Amphidecta, Auca, Spinantenna, Manerebia, Idioneurula* and *Gyrocheilus.* The antennae are generally two-fifths to half the length of the forewing costa. The antennal club is well developed, occupying the distal one-fifth to one-third of the antenna and between two and five times the thickness of the shaft. The third segment of the palpus is long for the Satyrini-section, never less than one-fourth as long as the second segment and frequently over half as long as the second in such genera as *Lasiophila* and *Idioneurula.*
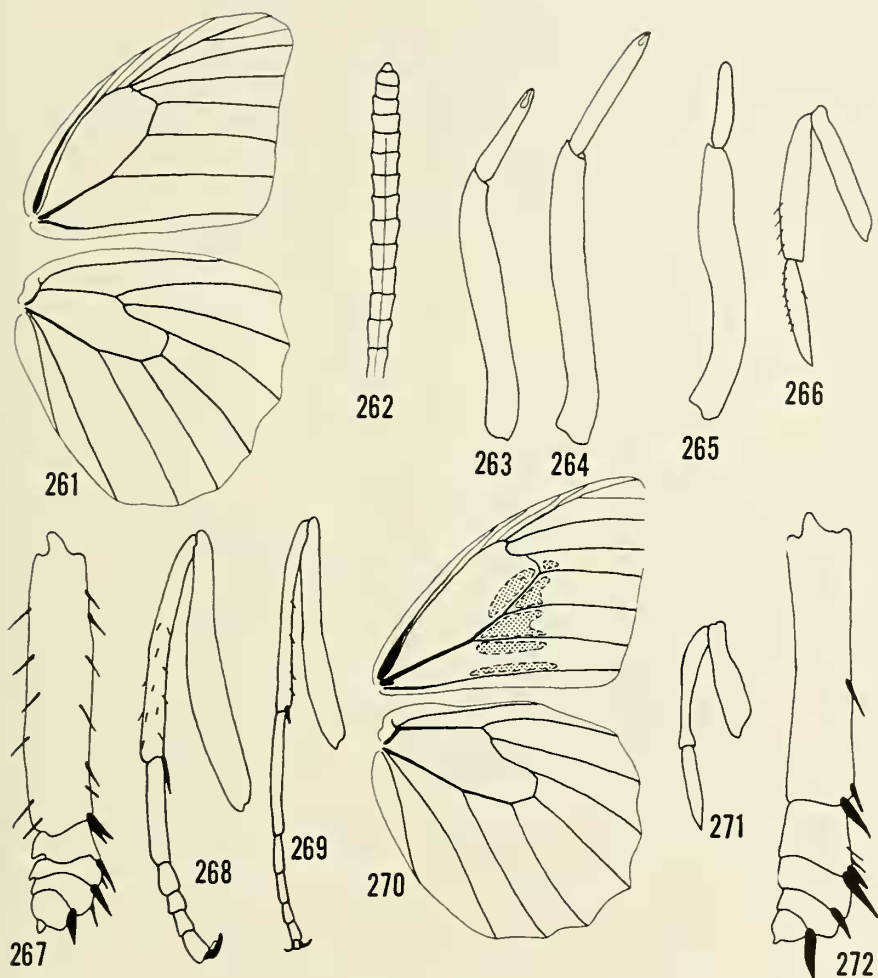
Figs. 261-272.   Satyrinae: Pronophilini.   261. *Pronophila thelebe* Double-
day and Hewitson, ♂ venation.   262. *P. thelebe*, antennal club.   263. *P. the-
lebe*, palpus.   264. *Drucina leonata* Butler, palpus.   265. *Amphidecta pignera-
tor* Butler, palpus.   266. *P. thelebe*, ♂ foreleg.   267. *P. thelebe*, ♀ foretarsus.
268. *P. thelebe*, midleg.   269. *A. pignerator*, midleg.   270. *Pedaliodes poesia*
(Hewitson), ♂ venation.   271. *P. poesia*, ♂ foreleg.   272. *P. poesia*, ♀ fore-
tarsus.

The hairs on the second palpal segment are highly variable in their
lengths: in such genera as *Eteona* and *Dioriste* the hairs are less
than twice as long as the segment is wide, whereas in other genera,

such as *Gyrocheilus* and *Manerebia,* the hairs may be as much as five
times the width of the segment.

The male foreleg is moderately well developed in most genera
with one (rarely two) tarsal subsegments that are devoid of spines
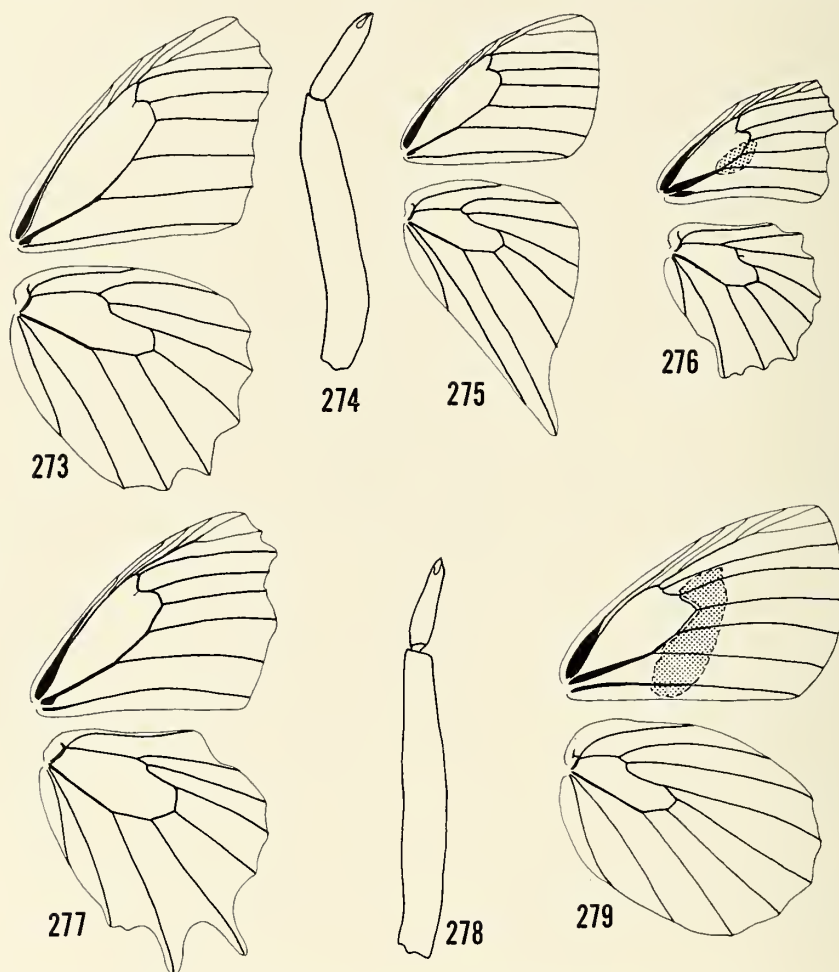
Figs. 273-279. Satyrinae: Pronophilini. 273. *Catargynnis pholoe* (Stau-
dinger), ♂ venation. 274. *C. pholoe,* palpus. 275. *Corades enyo* Hewitson,
♂ venation. 276. *Steroma bega* Westwood, ♂ venation. 277. *Daedalma
dinias* Hewitson, ♂ venation. 278. *D. dinias,* palpus. 279. *Argyrophorous
argenteus* Blanchard, ♂ venation.

(except in such genera as *Cheimas, Gyrocheilus* and *Pronophila*). The tibia is usually equal to, or longer than, the femur. Members of the *Lymanopoda*-series have greatly reduced forelegs with a mono-merous, unspined tarsus, and the femur is longer than the tibia. The female foreleg is usually moderately well developed with a penta-merus, clubbed tarsus bearing spines on the first four subsegments, but the foreleg of *Gyrocheilus* is greatly reduced with two unspined tarsal subsegments (Fig. 283). The relative lengths of the mid- and hindlegs are variable (Fig. 260). The mid-tibia is rarely less than twice as long as the first mid-tarsal subsegment, and it is gen-erally spiny dorsad, but smooth in such diverse genera as *Amphidecta* and *Penrosada*. The tibial spurs are present and well developed, and there is no spine at the dorsal, distal end of the midtibia.

The forewing cell is usually excavate and half to three-fifths the length of the forewing costa. The forewing radial veins arise in three branches from the cell in most genera, but in such genera as *Calisto, Steroma* and *Argyrophorus* the radials arise in two, or even a single, stems; veins Rs and M_1 arise connately (*Idioneurula*, etc.) to widely separate (as *Gyrocheilus* and *Pedaliodes*). Vein M_2 usually
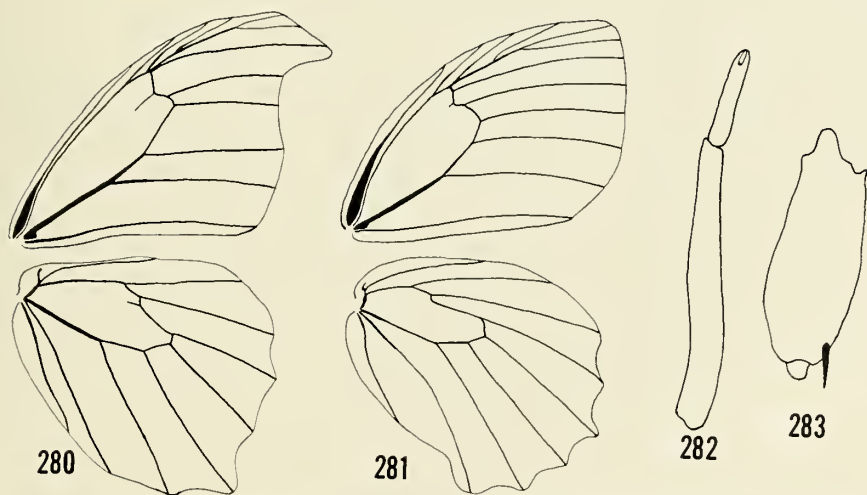
Figs. 280-283. Satyrinae: Pronophilini. 280. *Proboscis propylea* (Hew-itson), ♂ venation. 281. *Gyrocheilus patrobas* (Hewitson), ♂ venation. 282. *G. patrobas*, palpus. 283. *G. patrobas*, ♀ foretarsus.

arises midway between M_1 and M_3 (but much nearer M_1 in the *Lymanopoda*-series), and Cu_1 arises nearer M_3 than Cu_2 in some genera, midway between the two veins in some and nearer Cu_2 in others. Forewing vein Sc is always inflated, often greatly distended, and the other stalks may also be—all stalks are inflated in such genera as *Steroma* and *Spinantenna,* for example.

The hindwing cell is produced by the distad displacement of m_2-m_3 and half to over three-fifths the length of the wing measured to the end of M_3. Vein $Sc + R_1$ usually is longer than 3A, and M_3 and Cu_1 are well separated at their origins. Vein M_2 arises nearer, generally much nearer, M_3 than M_1.

The pattern is variable and highly modified, and there is convergence between some of the *Lymanopoda*-series and the Holarctic *Erebia.* Most of the species are figured by Weymer, 1912 (1910-1912).

Genera Included in the Pronophilini [2]

[2] Several genera have not been seen or were described too recently for critical inclusion in this revision. From the original descriptions it has, however, been possible to place them in their taxonomic positions. Such genera are preceded by an asterisk (*).

Pronophila-series, *sensu stricto*

*Altopedaliodes Forster, 1964: 148. Type-species: *Pronophila tena* Hewitson, by original designation.

Amphidecta Butler, 1867a: 404. Type-species: *Amphidecta pignerator* Butler, by monotypy.

*Antopedaliodes Forster, 1964: 151. Type-species: *Pedaliodes antonia* Staudinger, by original designation.

Calisto Hübner, 1816(1806-1838): 16. Type-species: *Calisto zangis* Hübner, designated by Butler, 1868a: 194.

Catargynnis Röber, 1892: 284. Type-species: *Daedalma pholoe* Staudinger, designated by Hemming, 1943: 23.
> =*Pseudomaniola* Röber, 1892: 222. Type-species: *Daedalma pholoe* Staudinger, by original designation. Preoccupied by *Pseudomaniola* Weymer, 1890.

Cheimas Thieme, 1906: 175. Type-species: *Oxeoschistus opalinus* Staudinger, by original designation.

Corades Doubleday, 1848a: 115. Type-species: *Corades enyo* Hewitson, by monotypy.

*Corderopedaliodes Forster, 1964: 155. Type-species: *Pedaliodes corderoi* Dognin, by original designation.
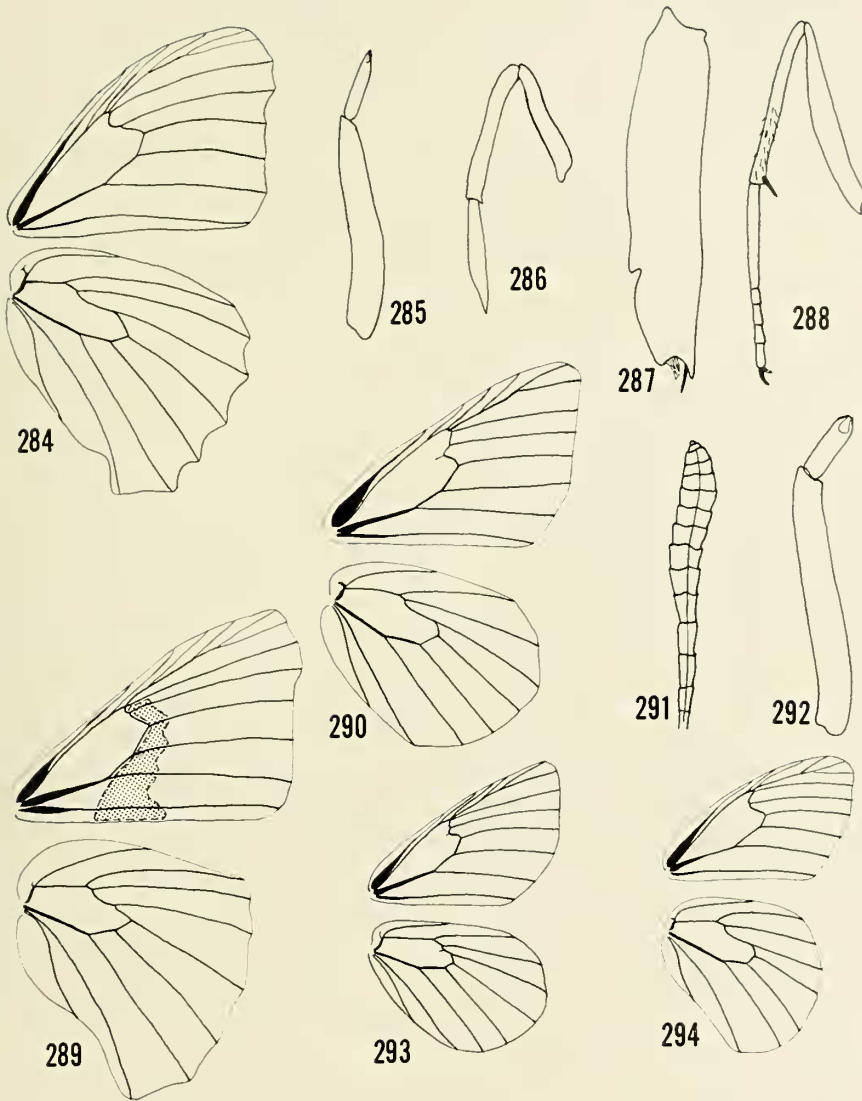
Figs. 284-294. Satyrinae: Pronophilini. 284. *Elina vanessoides* Blanch-
ard, ♂ venation. 285. *E. vanessoides,* palpus. 286. *E. vanessoides,* ♂ fore-
leg. 287. *E. vanessoides,* ♀ foretarsus. 288. *E. vanessoides,* midleg. 289.
Spinantenna tristis (Guérin), ♂ venation. 290. *Lymanopoda samius* West-
wood, ♂ venation. 291. *L. samius,* antennal club. 292. *L. samius,* palpus.
293. *Idioneurula erebioides* (Felder and Felder), ♂ venation. 294. *Manerebia
cyclopina* Staudinger, ♂ venation.

Daedalma Hewitson, 1858(1856-1876): [85]. Type-species: *Daedalma dinias* Hewitson, designated by Butler, 1867f: 268.

Dioriste Thieme, 1906: 171. Type-species: *Pronophila tauropolis* Westwood, by original designation.

Drucina Butler, 1872: 72. Type-species: *Drucina leonata* Butler, by monotypy.

Eretris Thieme, 1905: 131. Type-species: *Pronophila decorata* Felder and Felder, designated by Hemming, 1943: 24.

Eteona Westwood, 1850, *in* Doubleday, Westwood and Hewitson, 1846-1852: 254. Type-species: *Euterpe tisiphone* Boisduval, by monotypy.

Gyrocheilus Butler, 1867f: 267. Type-species: *Pronophila patrobas* Hewitson, by original designation. This name was misspelled "*Geirocheilus*" by Holland, 1898: 211.

Lasiophila Felder and Felder, 1859: 325. Type-species: *Lasiophila cirta* Felder and Felder, designated by Scudder, 1875a: 203.

*Muscopedaliodes Forster, 1964: 153. Type-species: *Pedaliodes muscosa* Thieme, by original designation.

Oxeoschistus Butler, 1867f: 268. Type-species: *Pronophila puerta* Hewitson, by original designation.

Panarche Thieme, 1906: 228. Type-species: *Corades tricordata* Hewitson, by original designation.

*Panyapedaliodes Forster, 1964: 157. Type-species: *Pronophila panyasis* Hewitson, by original designation.

*Parapedaliodes Forster, 1964: 153. Type-species: *Pronophila parepa* Hewitson, by original designation.

Pedaliodes Butler, 1867f: 267. Type-species: *Pronophila poesia* Hewitson, by original designation.

*Pherepedaliodes Forster, 1964: 149. Type-species: *Pedaliodes pheretiades* Smith and Kirby, by original designation.

*Physcopedaliodes Forster, 1964: 152. Type-species: *Pronophila physcoa* Hewitson, by original designation.

Polymastus Thieme, 1906: 138. Type-species: *Daedalma doraete* Hewitson, by original designation.

*Praepedaliodes Forster, 1964: 152. Type-species: *Pronophila phanias* Hewitson, by original designation.

*Praepronophila Forster, 1964: 182. Type-species: *Pedaliodes emma* Staudinger, by original designation.

Proboscis Thieme, 1906: 168. Type-species: *Pronophila propylea* Hewitson, by original designation.

Pronophila Doubleday and Hewitson, 1849, *in* Doubleday, Westwood and Hewitson, 1846-1852: pl. 60. Type-species: *Pronophila thelebe* Doubleday and Hewitson, designated by Butler, 1867f: 266.

   =*Mygona* Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852: 357. Type-species: *Pronophila thelebe* Doubleday, designated by Hemming, 1939: 133.

Pseudosteroma Weymer, 1912(1910-1912): 241. Type-species: *Steroma pro-*

nophila Felder and Felder, designated by Hemming, 1943: 25.

Punapedaliodes Forster, 1964: 148. Type-species: *Pedaliodes albopunctata* Weymer, by original designation.

Steremnia Thieme, 1905: 137. Type-species: *Pedaliodes (?) polyxo* Godman and Salvin, designated by Hemming, 1943: 25.

Steroma Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-1852: 400. Type-species: *Steroma bega* Westwood, by monotypy.

Steromapedaliodes Forster, 1964: 148. Type-species: *Pedaliodes albonotata* Godman, by original designation.

Thiemeia Weymer, 1912(1910-1912): 267. Type-species: *Pronophila phoronea* Doubleday, designated by Hemming, 1943: 25.

Elina-series

Argyrophorus Blanchard, 1852: 30. Type-species: *Argyrophorus argenteus* Blanchard, by monotypy.

Auca Hayward, 1953: 30. Type-species: *Satyrus pales* Philippi, by original designation.

Elina Blanchard, 1852: 28. Type-species: *Elina vanessoides* Blanchard, designated by Butler, 1868a: 194.

Haywardella Herrera, 1966: 71. Type-species: *Satyrus thione* Berg, by original designation.

Nelia Hayward, 1953: 42. Type-species: *Satyrus nemyroides* Blanchard, by original designation.

Neomaenas Wallengren, 1858: 78. Type-species: *Neomaenas servilaea* Wallengren, by monotypy.

   =*Stibomorpha* Butler, 1874: 204. Type-species: *Stibomorpha decorata* Butler (=*Neomaenas servilaea* Wallengren), by original designation.

Neosatyrus Wallengren, 1858: 79. Type-species: *Neosatyrus ambiorix* Wallengren, by monotypy.

Pampasatyrus Hayward, 1953: 28. Type-species: *Epinephele gyrtone* Berg, by original designation.

Pseudomaniola Weymer, 1890: 107. Type-species: *Pseudomaniola euripides* Weymer, designated by Hemming, 1943: 25.

   =*Neomaniola* Hayward, 1949: 156. Type-species: *Pseudomaniola euripides* Weymer, by original designation. Proposed to replace *Pseudomaniola* Weymer, wrongly believed to be preoccupied.

Quilaphoethosus Herrera, 1966: 69. Type-species: *Satyrus monachus* Blanchard, by original designation.

Spinantenna Hayward, 1953: 38. Type-species: *Satyrus tristis* Guérin, by original designation.

Stuardosatyrus Herrera and Etcheverry, 1965: 74. Type-species: *Argyrophorus williamsianus* Butler, by original designation.

Lymanopoda-series

Chillanella Herrera, 1966: 71.   Type-species: *Faunula stelligera* Butler, by
    original designation.
Cosmosatyrus Felder and Felder, 1867(1864-1867): 495.   Type-species: *Cos-*
    mosatyrus leptonenroides Felder and Felder, designated by Butler,
    1868b: 59.   Herrera (1965: 70) lists the type of this genus as "*Cos-*
    mosatyrus chiliensis chiliensis C. et R. Felder", but *chiliensis* is a Guérin
    name.   In any event, the type was properly designated by Butler.
Etcheverrius Herrera, 1965: 62.   Type-species: *Satyrus chiliensis* Guérin, by
    original designation.
Faunula Felder and Felder, 1867(1864-1867): 488.   Type-species: *Faunula*
    leucoglene Felder and Felder, by monotypy.
Homoeonympha Felder and Felder, 1867(1864-1867): 487.   Type-species:
    Homoeonympha pusilla Felder and Felder, by monotypy.
Idioneurula Strand, 1942: 389.   Type-species: *Idioneura erebioides* Felder
    and Felder, by original designation.
        =*Idioneura* Felder and Felder, 1867(1864-1867): 474.   Type-species:
        Idioneura erebioides Felder and Felder, by monotypy.   Preoccu-
        pied by *Idioneura* Selys, 1860.
Lymanopoda Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-
    1852: 401.   Type-species: *Lymanopoda samius* Westwood, designated
    by Butler, 1868a: 196.
Manerebia Staudinger, 1897: 139.   Type-species: *Manerebia cyclopina* Stau-
    dinger, designated by Hemming, 1943: 24.
Palmaris Herrera, 1965: 67.   Type-species: *Hipparchia monticolens* Butler, by
    original designation.
Penrosada Brown, 1944: 255.   Type-species: *Lymanopoda leaena* Hewitson,
    by original designation.
Sabatoga Staudinger, 1897: 143.   Type-species: *Sabatoga mirabilis* Stau-
    dinger, by monotypy.
Sarromia Westwood, 1851, *in* Doubleday, Westwood and Hewitson, 1846-
    1852: 402.   Type-species: *Sarromia obsoleta* Westwood, by monotypy.
Stygnolepis Strand, 1942: 389.   Type-species: *Stygnus humilis* Felder and
    Felder, by original designation.
        =*Stygnus* Felder and Felder, 1867(1864-1867): 487.   Type-species:
        Stygnus humilis Felder and Felder, by monotypy.   Preoccupied by
        Stygnus Perty, 1833.
Tetraphlebia Felder and Felder, 1867 (1864-1867): 489.   Type-species: *Tetra-*
    phlebia germainii Felder and Felder, by monotypy.
Zabirnia Hewitson, 1877: 92.   Type-species: *Zabirnia zigomala* Hewitson (=
    Lymanopoda acraeida Butler), by monotypy.
        =*Trophonina* Röber, 1892: 222.   Type-species: *Lymanopoda acrae-*
        ida Butler, by original designation.

Tribe SATYRINI Boisduval, 1836

(Figures 295-308)

Satyrides Boisduval, 1836: 166.
=Hipparchiadae Kirby, 1837: 297.

This tribe is at the center of its section, showing relationships with the Dirini by virtue of the general facies and the presence of the heavy spine at the dorsal, distal end of the midtibia, and with the Pronophilini and much of the Hypocystini in the shape of the hindwing cell. Through *Davidina* there is a progressive gradation from typical Satyrini to the Melanargiini.

Fig. 295. Satyrinae: Satyrini. Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera. In all instances the ML value is unity. The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

The weakly developed forelegs of both sexes serve to distinguish this tribe from the Hypocystini and much of the Pronophilini, and the production of the hindwing crossvein m_2-m_3 at M_2 will distinguish the satyrines from Melanargiini, Dirini and Erebiini. The most char-

acteristic features, however, of the Satyrini are on the midleg: all genera except *Chionobas* and *Oeneis* have a heavy spine at the dorsal, distal end of the midtibia, and in all genera but the *Oeneis*-series and *Davidina* the midtibia is less than one and one-fourth times as long as (and often shorter than) the first midtarsal subsegment.

All members of the Satyrini are Holarctic. The *Oeneis*-series is found throughout the Holarctic, but the *Satyrus*-series is almost exclusively Palearctic: only *Neominois* is known from North America.

There is a very interesting pattern similarity between the European genus *Minois* and the North American *Cercyonis*, but while the European butterflies belong to the present tribe, *Cercyonis* is a member of the Maniolini. Several authors (e.g., Hemming, in press) have considered *Cercyonis* synonymous with *Minois*, but structural examination of the two genera does not confirm this conclusion, as noted in the discussion of Maniolini.

Davidina is intriguing. Several authors have claimed it was a pierid, but examination of the tarsal claws shows *Davidina* to be a satyrid. Pierid tarsal claws are characteristically bifid (see Schatz and Röber, 1892), whereas those of *Davidina* are simple, as in most other satyrids.

Two series are recognized in the Satyrini, as follows:

The *Satyrus*-series, *sensu stricto*, distinguished by the extremely short midtibia and the presence of a heavy spine on the dorsal, distal end of the midtibia.

The *Oeneis*-series, distinguished by the longer midtibia lacking the spine at the dorsal, distal end.

The Satyrini are characterized as follows:

The eyes are naked. The antennae are more than two-fifths, but less than half, the length of the forewing costa. The antennal club is well developed, occupying the distal one-fourth to one-fifth of the antenna and three to more than five times as thick as the shaft (Fig. 297). The third segment of the palpus is short, generally one-fourth to one-fifth as long as the second segment. The hairs of the second palpal segment are long, two and a half to five times as long as the segment is wide.

The male foreleg is greatly reduced, the tibia and femur are of about the same length and the tarsus is mono- to trimerous without spines (Figs. 299, 306). The female foreleg is also greatly reduced, as much so as that of the male in several genera (Fig. 295), with
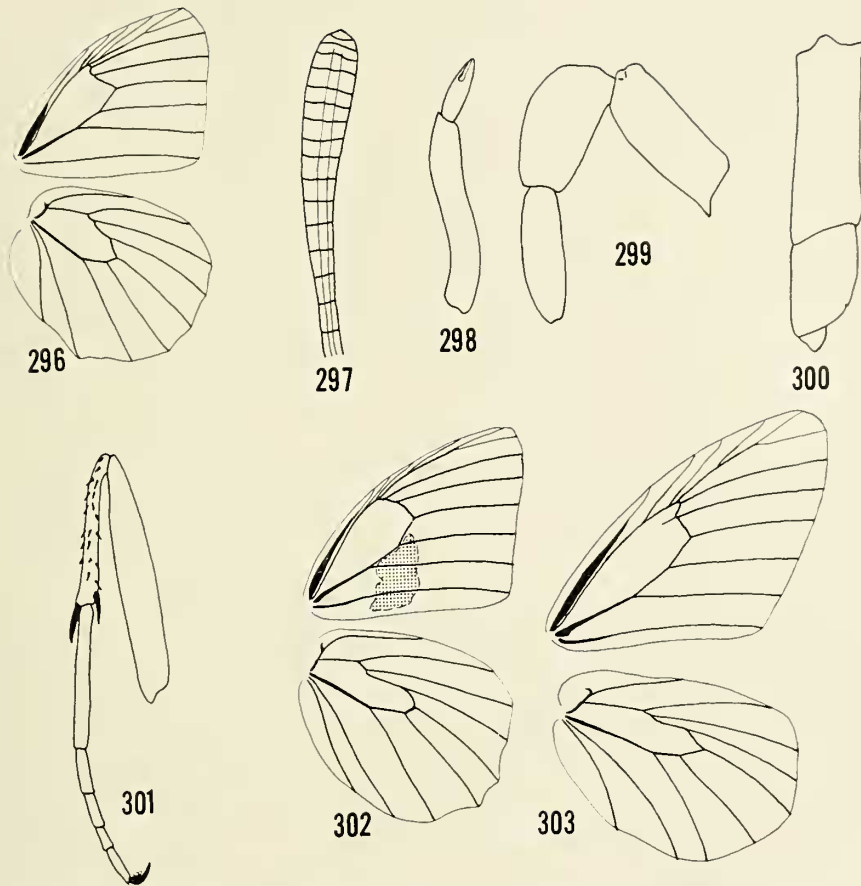
Figs. 296-303. Satyrinae: Satyrini. 296. *Satyrus actaea* (Linné), ♂ venation. 297. *S. actaea*, antennal club. 298. *S. actaea*, palpus. 299. *S. actaea*, ♂ foreleg. 300. *S. actaea*, ♀ foretarsus. 301. *S. actaea*, midleg. 302. *Brintesia circe* (Fabricius), ♂ venation. 303. *Neominois ridingsii* (Edwards), ♂ venation.

the tarsus unspined, or only weakly spined, and comprised of one to four subsegments. The hindleg is significantly longer than the mid-leg (Fig. 295). In most genera the midtibia is less than one and one-fourth times the length of the proximal midtarsal subsegment, but in *Davidina* and the *Oeneis*-series the midtibia is at least half again as long as the first midtarsal subsegment. The midtibia is very spiny dorsad, the spines being particularly heavy in this tribe, and the tibial spurs are present and well developed. There is a charac-teristic heavy spine at the dorsal, distal end of the midtibia in the

Satyrus-series (Fig. 301), which is absent in the *Oeneis*-series.

The forewing cell is square-cut to slightly excavate and half to almost three-fifths the length of the forewing costa. The forewing
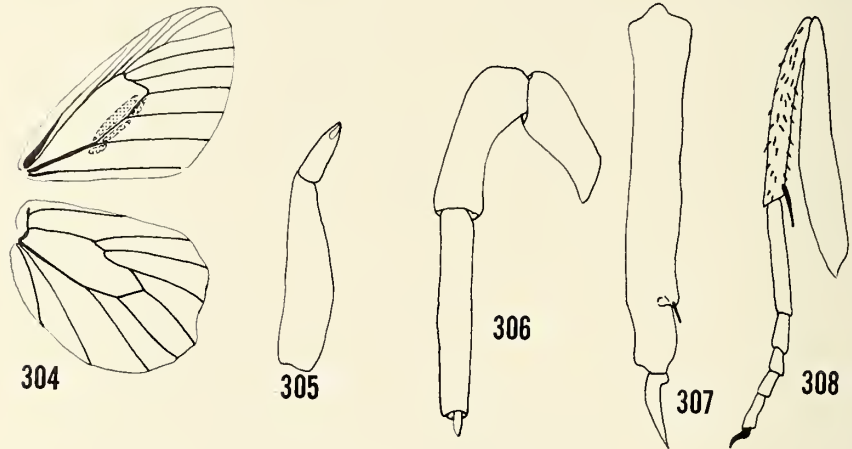
Figs. 304-308. Satyrinae: Satyrini, all *Oeneis norna* (Thunberg). 304. ♂ venation. 305. palpus. 306. ♂ foreleg. 307. ♀ foretarsus. 308. midleg.

radial veins arise from the cell in three branches, and veins Rs and M_1 arise separate, but they may be approximate. Vein M_2 arises nearer M_1 than M_3, and Cu_1 arises midway between M_3 and Cu_2, or slightly nearer the latter. Forewing vein Sc is inflated basad, but the other veins are little, if at all, thickened.

The hindwing cell is produced by the distad displacement of m_2-m_3 and half to three-fifths (slightly more in *Oeneis*) the length of the wing measured to the end of M_3. Veins $Sc + R_1$ and 3A are of about the same length, and M_3 and Cu_1 are well separated at their origins. Vein M_2 arises nearer M_3 than M_1.

The pattern is relatively uniform. The upper surface is shaded black, brown and/or orange and white with forewing ocelli in spaces M_1-M_3 and Cu_2-2A. The under surface pattern repeats the forewing ocelli, and the hindwings are cryptically marked. *Davidina* is white or off-white with dark brown to black veinal and interveinal lines. Illustrations of many of the species are given by Moore, 1893(1890-1893).

Genera Included in the Satyrini

Satyrus-series, *sensu stricto*

Arethusana de Lesse, 1951: 40. Type-species: *Papilio arethusa* Esper, by original designation.

Aulocera Butler, 1867b: 121. Type-species: *Satyrus brahminus* Blanchard, designated by Butler, 1868a: 194.

Berberia de Lesse, 1951: 41. Type-species: *Satyrus abdelkader* Pierret, by original designation.

Brintesia Fruhstorfer, 1912(1912-1915): 307. Type-species: *Papilio circe* Fabricius, by original designation.

Chazara Moore, 1893(1890-1893): 21. Type-species: *Papilio briseis* Linné, by original designation.

Davidina Oberthür, 1879: 19. Type-species: *Davidina armandi* Oberthür, by monotypy.

Eumenis Hübner, [1819](1816-1826): 58. Type-species: *Papilio autonoe* Esper, designated by Grote, 1873: 62.

Hipparchia Fabricius, 1807: 281. Type-species: *Papilio fagi* Scopoli, designated by Butler, 1868a: 194.
> =*Nytha* Billberg, 1820: 77. Type-species: *Papilio hermione* Linné (=*Papilio fagi* Scopoli), designated by Scudder, 1875a: 231.
> =*Melania* Sodoffsky, 1837: 81. Type-species: *Papilio fagi* Scopoli, by original designation. Preoccupied by *Melania* Lamarck, 1799. Proposed to replace *Hipparchia* Fabricius, wrongly believed to be preoccupied.

Kanetisa Moore, 1893(1890-1893): 42. Type-species: *Hipparchia digna* Marshall, by original designation.

Karanasa Moore, 1893(1890-1893): 38. Type-species: *Satyrus huebneri* Felder, by original designation.

Minois Hübner, [1819](1816-1826): 57. Type-species: *Papilio phaedra* Linné (=*Papilio dryas* Scopoli), designated by Butler, 1868a: 194.

Neohipparchia de Lesse, 1951: 40. Type-species: *Papilio statilinus* Hufnagel, by original designation.

Neominois Scudder, 1875b: 241. Type-species: *Satyrus ridingsii* Edwards, by original designation.

Paroeneis Moore, 1893(1890-1893): 36. Type-species: *Chionobas pumilus* Felder, by original designation.

Philareta Moore, 1893(1890-1893): 23. Type-species: *Papilio hanifa* Nordmann (=*Papilio anthe* Ochsenheimer), by original designation.

Pseudochazara de Lesse, 1951: 42. Type-species: *Satyrus pelopea* Klug, by original designation.

Pseudotergumia Agenjo, 1947: unnumbered page at end. Type-species: *Papilio phidia* Linné, by original designation.

Satyrus Latreille, 1810: 355. Type-species: *Papilio actaea* Linné, designated

by the action of the International Commission on Zoological Nomenclature, 1943, Opinion 142.

Oeneis-series

Chionobas Boisduval, [1833](1832-1843): 182.   Type-species: *Papilio aello* Hübner (=*Papilio glacialis* Moll), designated by Blanchard, 1840: 457.
Oeneis Hübner, [1819](1816-1826): 58.   Type-species: *Papilio norna* Thunberg, designated by Butler, 1868a: 196.

Tribe MELANARGIINI Verity, 1920
(Figures 309-314)

Melanargiinae Verity, 1920: 56.
=Agapetinae Verity, 1953: 3, 46.

This tribe contains some of the most distinctive of all satyrids, the pattern being unmistakable.   In the shape of the hindwing cell, morphology of the legs and general facies (excluding the white ground
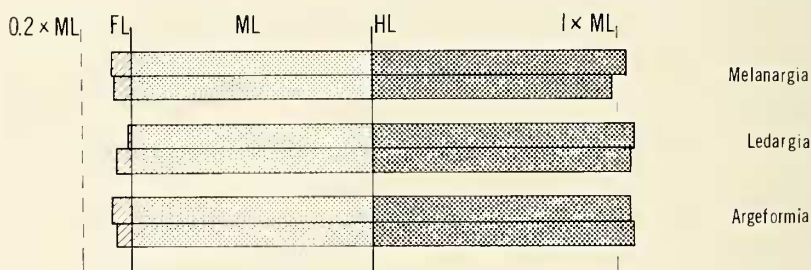
Fig. 309.   Satyrinae: Melanargiini.   Relative lengths of the femur + tibia + tarsus of the forelegs (FL, diagonal lines), midlegs (ML, light stippling) and hindlegs (HL, heavy stippling) of selected genera.   In all instances the ML value is unity.   The top bar for each genus represents the measurements obtained from males, the bottom bar those from females.

color), these butterflies closely resemble the Dirini and probably developed from a common stock with them.   The spiny legs, reduction of the forelegs and other structures suggest a strong affinity of the melanargiines and the Satyrini.   There is little to relate this tribe closely either to the Hypocystini or to the pronophilines.

The pattern of these butterflies sets them apart from all relatives —white with black marbling and well developed sets of ocelli on both wings, particularly the hindwings.

All members of the Melanargiini are found in the Palearctic from

Europe to China and Manchuria. There are more species in Asia than in Europe. The Melanargiini are characterized as follows:

The eyes are naked. The antennae vary little from half the length of the forewing costa. The antennal club is rather weakly developed, less than two to less than three times the thickness of the shaft. The third segment of the palpus is one-third to one-fourth the length of the second segment. The hairs of the second segment of the palpus are about four times as long as the segment is wide.

The male foreleg is greatly reduced, with a single, unspined tarsal subsegment; the femur is longer than the tibia (Fig. 312). The female foreleg is as reduced as that of the male with a monomerous, unspined tarsus (Fig. 313). The relative reduction of the fore-, mid- and hindlegs is shown in Fig. 309. The midlegs are usually shorter than the hindlegs (Fig. 309). The midtibia ranges from just under to just over one and a half times as long as the proximal midtarsal
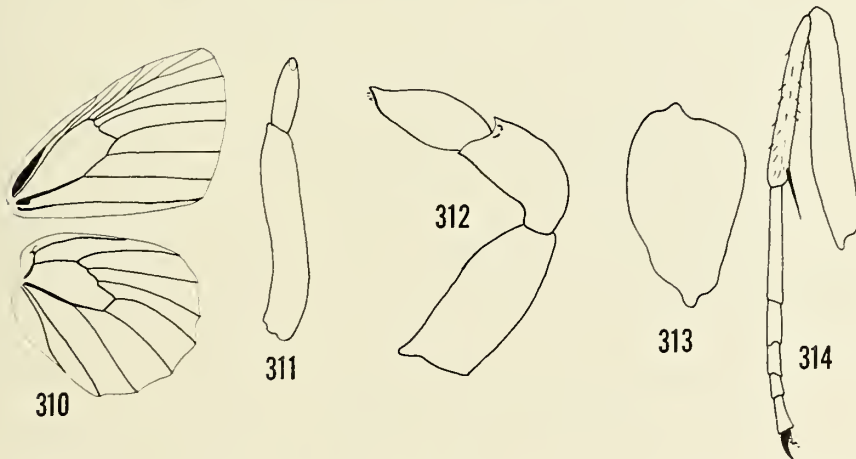
Figs. 310-314. Satyrinae: Melanargiini, all *Melanargia galathea* (Linné). 310. ♂ venation. 311. palpus. 312. ♂ foreleg. 313. ♀ foretarsus. 314. midleg.

subsegment and is very spiny dorsad. The tibial spurs are present and well developed; there is no heavy spine at the dorsal, distal end of the midtibia.

The forewing cell is square-cut and approximately half the length of the forewing costa. The forewing radial veins arise in three branches from the cell, and veins Rs and M_1 are separate, but may

be approximate, at their origins. Vein M_2 arises much nearer M_1 than M_3, and Cu_1 arises nearer M_3 than Cu_2. If any forewing veins are inflated, only Sc would be, and that not extensively.

The hindwing cell is produced at the origin of M_3 and half to three-fifths the length of the wing measured to the end of M_3. Veins $Sc + R_1$ and 3A are of about the same length, and M_3 and Cu_1 are well separated at their origins. Vein M_2 arises slightly nearer M_1 than M_3.

The pattern is quite distinctive: all species are white or cream-colored marbled with black and with the ocelli well developed. Many genera have been named, but it seems that one genus would suffice biologically for all the species.

Genera Included in the Melanargiini

Argeformia Verity, 1953: 47. Type-species: *Papilio arge* Sulzer, by original designation. Proposed as a subgenus of *Agapetes* Billberg (=*Melanargia* Meigen).

Epimede Houlbert, 1922: 132, 142, 160. Type-species: *Arge halimede* Ménétriés, designated by Hemming, 1934a: 143.

Halimede Oberthür and Houlbert, 1922: 192. Type-species: *Halimede asiatica* Oberthür and Houlbert, by monotypy.

Lachesis Oberthür and Houlbert, 1922: 192. Type-species: *Lachesis ruscinonensis* Oberthür and Houlbert (=*Arge lachesis* Hübner), by original designation.

Ledargia Houlbert, 1922: 157. Type-species: *Melanargia leda* Leech, by original designation.

Melanargia Meigen, 1829: 97. Type-species: *Papilio galathea* Linné, designated by Kirby, 1894: 41.

    =*Arge* Hübner, [1819](1816-1826): 60. Type-species: *Papilio psyche* Hübner (=*Papilio occitanica* Esper), designated by Butler, 1868a: 196. Preoccupied by *Arge* Schrank, 1802. This name was suppressed in favor of *Melanargia* Meigen by the International Commission on Zoological Nomenclature, 1956, Opinion 400.

    =*Agapetes* Billberg, 1820: 78. Type-species: *Papilio galathea* Linné, designated by Scudder, 1875a: 104. This name was suppressed in favor of *Melanargia* Meigen by the International Commission on Zoological Nomenclature, 1956, Opinion 400.

Parce Oberthür and Houlbert, 1922: 193. Type-species: *Parce fergana* Oberthür and Houlbert (=*Melanargia parce* Staudinger), by original designation.

GENERA OF UNCERTAIN POSITION

Genus **Pamperis** Heimlich, 1959 (Fig. 315)

Pamperis Heimlich, 1959: 177. Type-species: *Pamperis poaoeneis* Heimlich, by original designation.
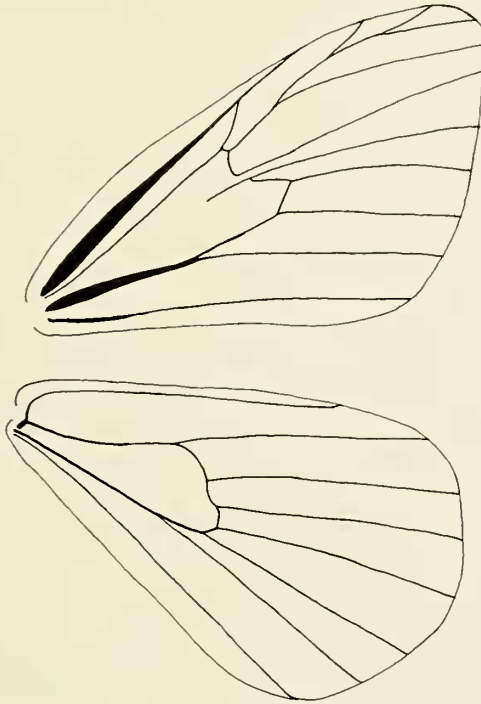
Fig. 315. Venation of *Pamperis poaoeneis* Heimlich (after Heimlich, 1959). Note the aberrant venation pattern discussed in the text.

Having seen no specimens of the type-species of this Neotropical monotypic genus, I can only evaluate its position in terms of the original description, which leaves many questions unanswered. Heimlich's photographs of the types suggest he was correct, at least superficially, in placing this genus near *Cosmosatyrus* Felder and Felder, and as such, it certainly belongs in the *Lymanopoda*-series of the satyrine tribe Pronophilini. However, the venational drawing given represents either an extraordinary aberration—the veins in the apical portion of the forewing are arranged like no known satyrid, and the hindwing lacks a major vein (Fig. 315)—or represent draft-

ing errors. Until these structures, as well as others not considered
in the original description, have been studied, it will be quite im-
possible to assign this genus to its proper position among the Satyridae.

Genus Setodocis Billberg, 1820

Setodocis Billberg, 1820: 78. Type-species: *Papilio periboea* Fabricius, de-
signated by Scudder, 1875a: 268.

I have no idea to what this genus refers, and neither does anyone
else; *periboea* is a "lost" species. The best opinion is that of Hem-
ming (in press), "Include at the end of the subfamily Mycalesinae as
a *genus dubium.*" The name is in the literature, so it must be men-
tioned here, but it would seem advisable to suppress it.

The Evolution and Zoogeography of the Satyridae

The twin subjects of evolution and biogeography have provided
biologists since the days of Charles Darwin and Alfred Russel Wal-
lace with the raw material for sundry mental gymnastics and manipu-
lations of the earth's flora, fauna, history and even crust through
space and time. Such exercises, while based on the best available
evidence, are limited by that evidence, and what are proposed as facts
must be considered in actuality only as more or less educated guesses.
The preceding statement is particularly true when one is dealing with
such insects as butterflies, the fossil records of which are almost non-
existent. In drawing evolutionary, and especially zoogeographic, in-
ferences it is necessary to guess the past history of butterflies by com-
parison with fossil histories of vertebrates and to interpret tendencies,
such as the simplification of structures through phylogenetic lines, by
the interpretations given such trends in groups with reasonably docu-
mented fossil records.

Zoogeography, in particular, has been a constant source of
controversy, with several opposing schools of thought attempting to
analyze distributional data in accordance with conflicting theories.
At present there are two major camps of biogeographers which may be
called the Wegener and the Matthew schools, although each theory
has been refined far beyond its originator's proposals.

"Nothing in zoogeography has brought forth more argument or
more demands for an open mind—the other man's mind—than the
idea of continental drift." (Darlington, 1957: 606). This theory,

first put forth by Wegener, states briefly that the continents were a single landmass which broke apart, and the pieces drifted across the relatively plastic mantle, chiefly during the Mesozoic and into the Tertiary, to their present positions. By rotating the present-day continents and fitting them together it is possible to arrive at a convincingly completed "jig-saw puzzle"; indeed, it was this sort of piecing together of the landmasses of the world which provided the basis for the theory in the first place. Caster (1952) summarized the stratigraphic evidence supporting connections between South America and Africa, particularly during the Mesozoic, and further cited the similarity between the shallow water invertebrates of the two continents, but Dunbar (1952: 154) demonstrated by the similarity of shallow water molluscs of Kwajalein, Bikini and Guam that many shallow water invertebrates can cross deep water "barriers", probably as free-swimming larvae. Darlington (1957: 607-608) showed another of the problems with the acceptance of the Wegener hypothesis as an explanation of the present-day animal distributions, when he stated, ". . . if a group of animals now occurs only in Africa and Brazil, it is said to date from and be evidence of a hypothetical African-Brazilian continent. This method depends on an assumption which Wegenerians usually do not put into words: that animal distributions are more permanent than land, that animals move less than continents." This argument more or less summarizes my own objections to continental drift as an explanation for the distributions of present-day organisms.

Most American zoogeographers today subscribe to the general theory of animal dispersal proposed by Matthew (1915) and elaborated upon by Hesse, Allee and Schmidt (1951) and Darlington (1957). Matthew set forth his thesis in the beginning of his paper (1915: 173).

While the details of Matthew's work have been refined, the general skeleton has remained intact. Geologic evidence, such as that presented by Schuchert (1935) for the history of the Neotropics, has strengthened the Matthew theory. Biogeographers have been better able to devote their attention to the more knotty problems of how, when and why organisms arrived where they are.

Since Schuchert (1935) showed the existence of several Tertiary "water gaps" between North and South America and roughly

dated them, many authors have considered it an absolute necessity to close these gaps physically so that organisms might cross them. This practice, however, has recently come under scrutiny from several authors, notably Simpson (1952), who demonstrated mathematically that given a length of time of sufficient duration and a sufficiently large "feeder" population even the most improbable dispersal of a terrestrial organism over water could be a virtual certainty. While this mathematical exposition does not serve as evidence of a population of an area *via* waif dispersal, it shows a method by which such dispersal could be accomplished. It is of great importance to the understanding of the aerial dispersal of such insects as butterflies because it shows that landmasses need never be physically connected to exchange faunal elements across barriers. Such studies indicate that reappraisals are in order concerning the necessity of erecting land bridges across ocean deeps. Certainly physical barriers work less hardship on such strong flying butterfly genera as *Danaus* (Danaidae), *Precis* and *Vanessa* (Nymphalidae), *Libythea* (Libytheidae) and *Leptotes* and *Lampides* (Lycaenidae) than on the more sedentary Satyridae and Ithomiidae.

I wish here to call attention to the second paragraph of Matthew's thesis (1915: 173). Nearly all the principal routes of migration pass through either the eastern Palearctic or the Indo-Malayan region. If a group is in a rather generalized condition at the time of its expansion, it seems illogical that such a group would not leave some more or less primitive members along its primary path of dispersal. In the case of biotic interchange between the Palearctic and the Nearctic, the Paleotropics and the Neotropics, Asia and Australia, Africa and Australia, these waves of dispersal would have extended through eastern Asia. Eastern Asia also provides the complete spectrum of biotopes, from Arctic tundra to tropical rainforest to the most arid desert—a prospective "home" for almost any group. No other region on earth is fed by so many major routes of dispersal, hence, no other region should be expected to have organisms derived from so many different sources. This diversity has led many students (*e.g.*, Darlington, 1957) to consider eastern Asia the major center of dispersal, a veritable "Garden of Eden". In the following pages I shall attempt to show that at least the Satyridae need not have *arisen* in this region, although eastern Asia certainly played an

important role in the subsequent evolution of the family.

Origin of the Satyridae

Consideration of the origin and subsequent evolution of the Satyridae must be prefaced by a discussion of their relatives. Two nymphaloid families, the Morphidae (including the Amathusiidae) and Ithomiidae, are closely allied to the family under consideration here and have been characterized at the beginning of the systematic revision. The evolution of all three families must be considered together to lay the groundwork for that which follows.

The living nymphaloid families divide basically into two major groups on larval foodplant requirements. With very few exceptions (Ehrlich and Raven, 1965) the "true" nymphalids feed on dicotyledonous plants, whereas the larvae of the satyrids utilize monocotyledons exclusively.

Forbes (1932) has assumed that the modern lepidopterous families had already differentiated by the Jurassic, and Carpenter (1930) felt that the Lepidoptera as an order could be traced only as far back as the Jurassic. Present evidence (Just, 1948) indicates that the proliferation and differentiation of the angiosperms took place in the late Mesozoic. The differentiation of the nymphaloid stock must have been somewhat synchronous with this proliferation of the flowering plants, but there is some question about this point. Fox (*in litt.*) feels that there is no reason to assume that morphological differentiation may not have preceded plant evolution, *i.e.,* present monocotyledon feeders may have begun as dicotyledon feeders, or *vice versa*. Whether plant or butterfly evolution came first becomes a moot point, but the potential new niche provided by the evolution of the two basic stocks of plants must have provided some impetus for the subsequent, if not the initial, evolution of the butterflies. In any event, the butterflies are a relatively recent group compared with the Orthoptera and the Odonata, which were well developed by the Carboniferous.

The Ithomiidae feed as larvae almost exclusively on the Solanaceae (Fox, 1956: 13) and belong on this basis to the "true" nymphalids, although they are not far removed from the satyrid complex. These butterflies have reached their highest development

in the Neotropics, although a single tribe, the Tellervini, is found in
Australia and New Guinea.

The Satyridae, *sensu stricto,* overwhelmingly feed as larvae on
Gramineae and Cyperaceae, and all known satyrids feed on mono-
cotyledons. Some members of the family feed on Palmaceae (*Elym-
nias* and relatives). All known brassolines feed on monocots,
generally utilizing the primitive ones, but a few also feed on bamboo;
none are known to use dicots. The brassolines are exclusively Neo-
tropical, none living farther north than Mexico. The foodplant
requirements of the other primitive Neotropical satyrids (Haeterinae
and Biinae) are unknown, but since they are restricted to the deep
forest they probably do not use grasses, other than possibly bamboo.
There are many other monocotyledons in the rainforest, and these
are probably the food plants.

Structurally, the Indo-Australian *Amathusia, Faunis, Taenaris,*
etc. belong with the American *Morpho* in the family Morphidae. All
the known Indo-Australian Morphidae feed on monocotyledons as
larvae, many using Gramineae. In the New World, however, the
morphids (represented only by the nominate genus) predominantly
feed on dicotyledonous plants of the family Canellaceae, Myrtaceae,
Menispermiaceae, Rhamnaceae, Sapindaceae and Leguminoseae.
One species, however, *Morpho aega* (Fabricius), feeds on bamboo
(Gramineae). *Morpho* is one of the few nymphaloid genera known
which utilizes both monocotyledons and dicotyledons as larval food;
indeed, the Morphidae is the only family commonly showing such
habits. It seems evolutionarily significant that the genus *Morpho* is
limited to the New World tropics. Furthermore, excluding the
brightly colored and highly modified upper surface of these butter-
flies, the morphids seem to typify the "primitive nymphalid pattern"
of Schwanwitsch (1924): most of the elements of the pattern are
present in the primitive species.

In summary, many of the most primitive members of various
nymphaloid families occur *only* in the Neotropics. The Neotropical
tribe Tithoreini of the Ithomiidae is as primitive as the Indo-
Australian Tellervini, and the two might well be combined were it
not for their geographic isolation and a few morphologic characters
(Fox, 1956: 20). As shown above, the Neotropical genus *Morpho*
is the most primitive of the morphids. The most primitive satyrids
are the Neotropical Haeterinae, which preserve the forewing vein 3A.
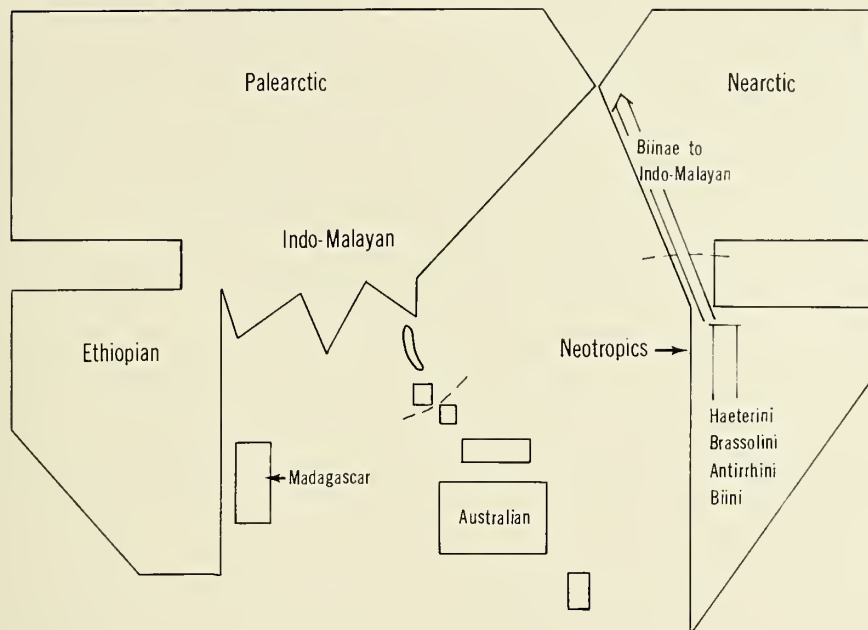
Fig. 316. The early distributional history of the Haeterinae, Brassolinae and Biinae in the New World. All movement illustrated in this figure was during the Cretaceous and earliest Tertiary (open arrows). In succeeding figures stippled arrows indicate mid-Tertiary movement, whereas solid black arrows indicate late Tertiary and Quaternary migration. Major areas of the world are indicated on this map for reference, and no attempt is made to present exact continental outlines at any given period of geologic time.

The next most primitive groups of satyrids are the biines and the brassolines and the majority of these, including the most primitive ones, are New World species. In addition to these satyrids, the most primitive danaids (*Clothilda* and the Lycoreinae) are found in Central America and the Antilles. The remaining danaids are derived from Paleotropical groups which arrived in the Neotropics much later.

In view of the evidence compiled in the preceding paragraphs, a feasible explanation of the evolution of the nymphaloid butterflies seems to require serious consideration of tropical America as something other than a receptacle for pre-existing Holarctic groups. Probably a relatively undifferentiated nymphaloid stock either entered the Neotropics as part of the extensive Holarctic invasion during the

Cretaceous (Darlington, 1957: 561-564), or this stock was already in tropical America prior to the connection of South America with the Holarctic. Since there are so many highly primitive groups of the Satyridae, Morphidae, Ithomiidae, and Danaidae in the Neotropics, it further appears that it was in tropical America that the fundamental bifurcation of the nymphaloid stock occurred. At least these four families appear to have arisen in the Neotropics. Later all four reinvaded the Holarctic, probably during the Cretaceous, but only two of them (Satyridae and Danaidae) reinvaded the American tropics during the Tertiary. The Tertiary history of the danaids probably parallels that of the satyrids, which will be discussed later. Endemic, primitive, though often highly specialized, stocks of all four families may be still found in the Neotropics. It seems most likely, therefore, that these families all arose in the Cretaceous (possibly earlier) rainforests of tropical America.

THE LATER HISTORY OF THE SATYRIDAE

The most primitive satyrids, the Haeterinae, are now restricted to the Neotropical rainforest, and there is no indication that they ever were elsewhere, and all evolution in this group has occurred within the American tropical forests (Fig. 316). No members entered the Old World, as did members of the Ithomiidae. It is also doubtful that these insects ever exploited the grasslands that resulted from progressive drying during the Tertiary. In fact, these insects are singularly well adapted to the deep forest—the hyaline wings of many species and the ghost-like fluttering flight render them virtually invisible except when they pass through patches of sunlight. Masters (*in litt.*) says that *Haetera* always restricts itself to the deepest forest, never entering sunlit areas, but I have seen species of *Pierella* and *Callitaera* sunning themselves early in the morning, but not later in the day.

Figs. 317, 318. Fig. 317. The origin and subsequent distributional history of the Melanitini (Biinae) and the origin of the Elymniinae from the Melanitini. For details, see text. Fig. 318. The origin and proliferation of the Elymniinae into the tribes Lethini (see Fig. 319), Elymniini (Fig. 320), Mycalesini (Fig. 321) and Zetherini. The latter tribe did not significantly leave the Indo-Malayan region. The probable origin of the Eritinae is also shown on this map. For details, see text.

New
World
biines

Elymniinae
Melanitini

317

Lethini (Fig. 319)
Elymniini (Fig. 320)
Mycalesini (Fig. 321)
Zetherini

Elymniinae

Satyrinae

Eritinae
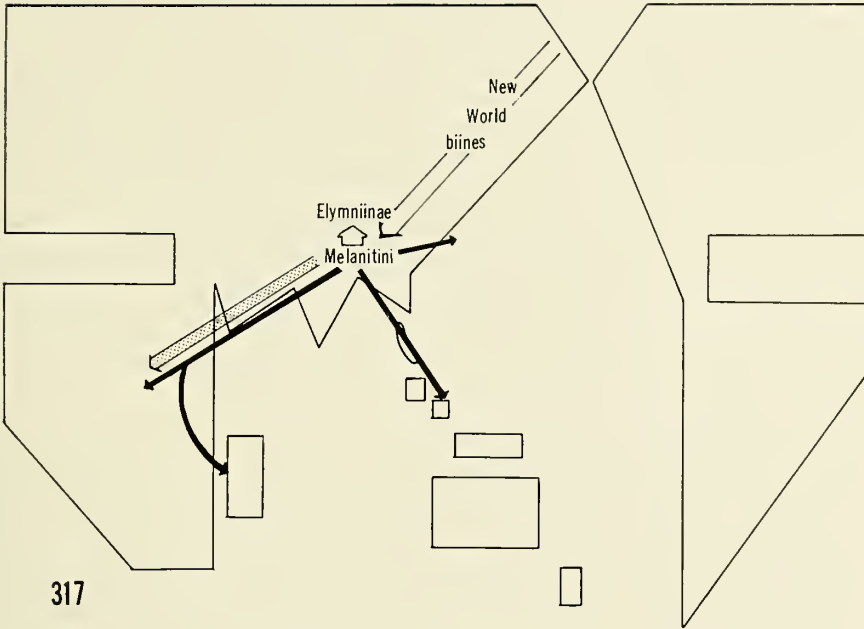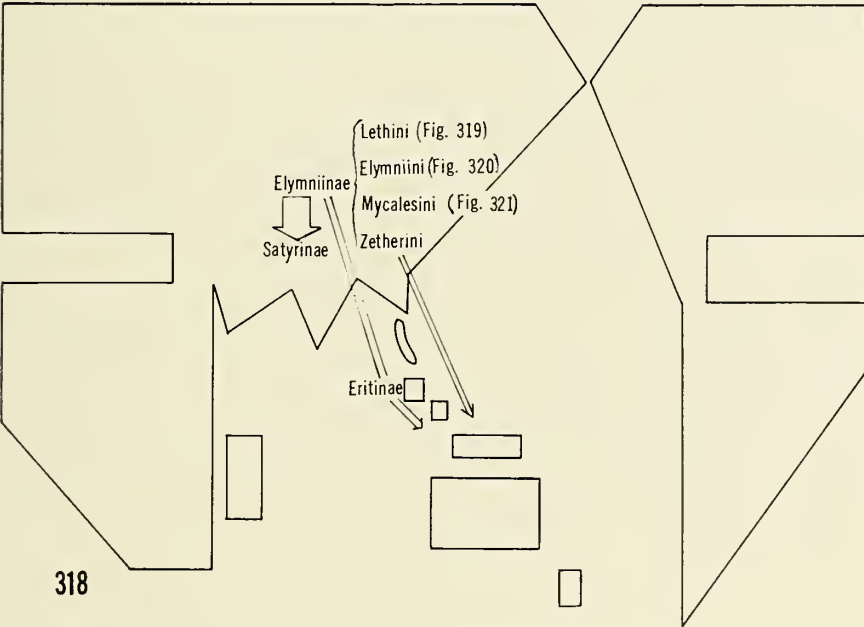
318

The history of the Brassolinae probably closely parallels that of the Haeterinae (Fig. 316). These butterflies, however, are strong fliers and have evolved a "flash coloration pattern" on the upper surface and a cryptic under surface. They do not depend so much on camouflage as on the strength of their flight. Many species are crepuscular, particularly those occurring in more open country, but most species are more or less restricted to the rainforest.

The Biinae did move into the Holarctic and apparently provided the basis for the evolution of the rest of the family. Those biines which did not leave the Neotropics (Fig. 316) have remained rainforest butterflies with patterns and flight characteristics similar to those of the brassolines.

Whether the Neotropical members of any of the preceding subfamilies ever invaded the grasslands is questionable. If they did, they were wiped out, probably in competition with the better adapted Satyrinae which later came into the New World. It seems more likely, however, that these butterflies never left the rainforest of their origin and evolved into such ecologically successful species that they easily resisted competition from the satyrines; perhaps these primitive groups actually forced the satyrines into more open country.

Those Biinae which did move into the Holarctic were obviously much more like Antirrhini than *Bia,* but there are now no New World antirrhines that have extremely close relationships with the Old World species. The migrating biines were forced into the Paleotropics at a fairly early time, where they apparently evolved into the present-day tribe Melanitini (Fig. 317). Several of the melanitines have become very widespread, apparently relatively recently, and one, *Melanitis leda* (Linné), is now found from West Africa to Madagascar and east into Australia and Japan. Most of the species are found in the Indo-Malayan region and in tropical Africa (Table 7). The Melanitini responded to the increase in aridity of the early Tertiary by invading open woodlands and even more open country, being thus the first satyrids, historically and evolutionarily, to leave the deep forest. These butterflies are more or less crepuscular, like the Brassolinae. A possible explanation for the crepuscular flight

Figs. 319, 320. Fig. 319. The distributional history of the Lethini. See text for details. Fig. 320. The distributional history of the Elymniini. See text for details.

319

Pararge-series

Iethine stock

Lethe-series

Aeropetes-series

320

Elymniini
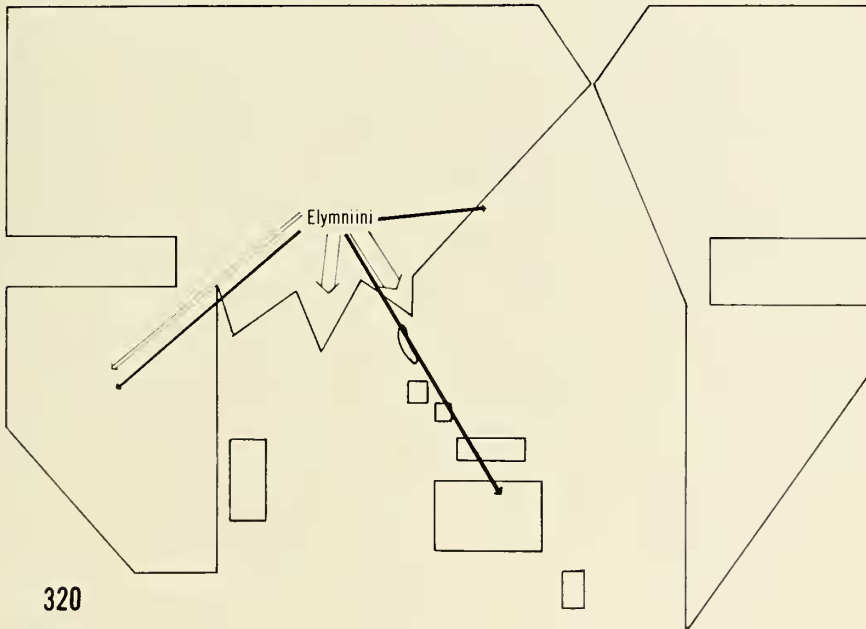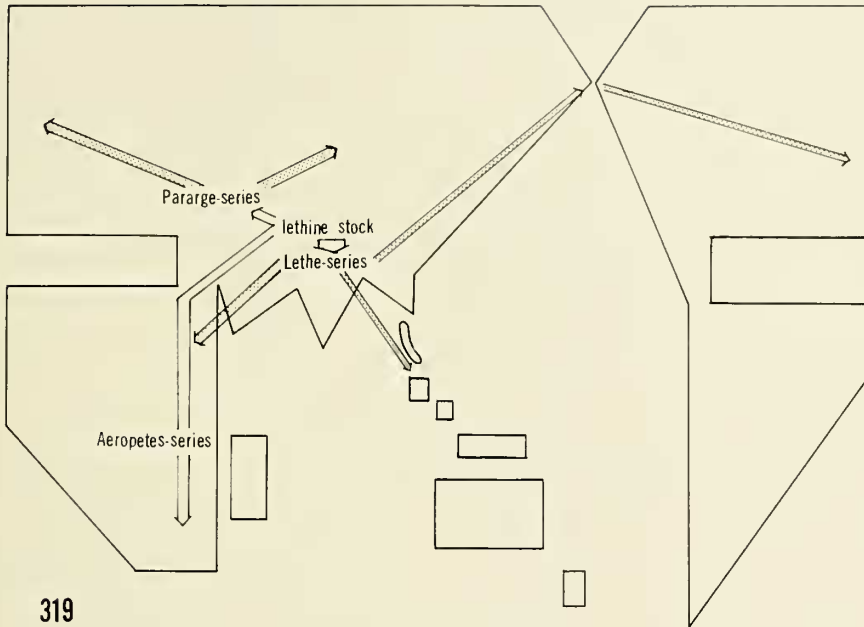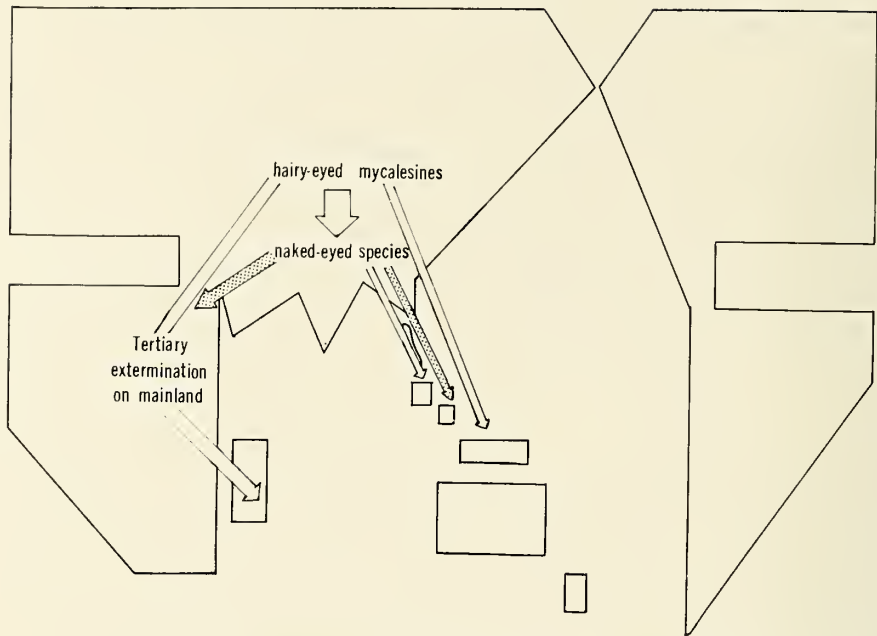
Fig. 321. The distributional history of the Mycalesini. See text for details.

habit is that such species are actually approximating the conditions of the deep forest as regards light intensity. In short, such species are basically forest species that are "carrying the forest environment with them". The successful invasion of the open country provided the impetus for the great adaptive radiation and phylogenetic diversification of the satyrids in the Old World. The Neotropical Antirrhini, on the other hand, never became successfully adapted to open country, and without leaving the forests evolved into the present tribe with fewer than twenty species. In the Indo-Australian region the Melanitini were probably giving rise, meanwhile, to the Elymniinae through steps resembling the present-day genera *Parantirrhoea* (Melanitini), *Ptychandra* and *Samanta* (both Lethini), shown in Figs. 317, 318.

The Elymniinae proliferated rapidly during late Cretaceous and early Tertiary into the four tribes, most of which stayed in the woodlands and scrublands: some (a number of Mycalesini) invaded the savannas, and others (the *Neorina*-series) re-entered the deep forests. · The pattern of early and later migration of the subfamily rather closely parallels that of many vertebrate groups and seems to have been

limited northward by the Tethys Sea. Little movement from the Paleotropics seems to have been accomplished before the closing of this "water gap" between the Paleotropics and the Palearctic (Fig. 318). Interrelationships within the Elymniinae can be better drawn than those within any other subfamily. The Lethini grade toward the Zetherini, on the one hand, and the Mycalesini (through such genera as *Mandarinia* and *Orsotriaena*), on the other, as brought out in the systematic revision. The Mycalesini connect well with the Elymniini, as do the zetherines. The elymniines are "throwbacks" in one respect: all known members feed as larvae on Palmaceae, hence the common name "palmflies". All tribes of the Elymniinae but the Zetherini are widely distributed in the Old World at present, although only one—the *Pararge*-section of the Lethini—has managed significantly to penetrate the Palearctic. The distributional histories of the tribes are shown in Figs. 319 (Lethini), 320 (Elymniini), 321 (Mycalesini); the actual patterns are discussed in the analyses of the individual faunae of the world.

Apparently within a short time—probably still in the Cretaceous —the Elymniinae gave rise to the Satyrinae (Figs. 318, 322), presumably through either the Mycalesini or (more probably) the Lethini and the Hypocystini of the Satyrinae. It is also probable that the Eritinae arose from a basic elymniine stock (Fig. 318) and possible that the Ragadiinae did (Fig. 322), but the origin of the latter subfamily is among the most obscure in the family Satyridae.

The hypocystine genus *Lamprolenis,* while a fairly typical member of that tribe, retains some very primitive characteristics similar to those of the Mycalesini (Fig. 148). There is a typical *Mycalesis*-like hair tuft on the hindwing, and the general facies embody a combination of mycalesine and hypocystine characteristics.

The other case of similarity between the Elymniinae and Satyrinae is to be found in South Africa, where members of the *Aeropetes*-series of the Lethini seem to grade into the Dirini (Figs. 67-72 and 248-259, respectively). It would be tempting to ascribe great evolutionary significance to the similarity, but the *Aeropetes*-series contains primitive lethines, whereas the Dirini appear to be fairly advanced Satyrinae—particularly as regards the reduction of the forelegs of both sexes. Therefore, this similarity is ascribed to convergence, not to phyletic proximity.

The strongest link between the Elymniinae and the satyrines occurs through the subfamily Eritinae. Eritines have many characteristics in common with the Lethini, as discussed in the systematic revision, and also share characters with the Hypocystini. This cannot be merely convergence, and it appears that the Satyrinae arose in the Indo-Australian region from an elymniine stock not far removed from the lethine stock (Figs. 318, 322).

In any event, the Satyrinae—probably from a Hypocystini-like stock—soon split into two basic groups, the Ypthimini- and Satyrini-sections (Fig. 322). This dichotomy was probably brought about by the increasing aridity and proliferation of savannas during the early Tertiary. The Ypthimini-section generally occupies more open country than do the Satyrini-section butterflies.

During the early to mid-Tertiary the various tribes of the Satyrinae, except the Pronophilini and Euptychiini, probably evolved in the Old World (Figs. 323-326). Upon the reopening of the Central American land connection between North and South America— it was probably sufficiently opened in Miocene, perhaps Oligocene, times—the forerunners of the principal South American tribes of the Satyrinae, the Pronophilini (derived from the Satyrini-section, Fig. 325) and the Euptychiini (from the Ypthimini-section, Fig. 323) reentered South America and rapidly assumed dominance over the "old" South American fauna. At least part of this dominance may be ascribed to the ecological diversity shown by both tribes, as explained in the discussions of the tribes in the systematic revision. A glance at the numbers of species involved in both the Pronophilini and Euptychiini shows the dramatic radiation that has taken place in the Neotropics.

It is doubtful that the radiation of the Euptychiini and Pronophilini resulted in a wholesale extinction of the Haeterinae, Brassolinae and Biinae, since the new arrivals probably did not compete ecologically with the already established primitive ones. Both the Pro-

Figs. 322, 323. Fig. 322. The origin of the Satyrinae from the Elymniinae and the division of the satyrines into the Hypocystini, the Ypthimini-section and the Satyrini-section. The probable origin of the Ragadiinae from the Elymniinae is also shown in this figure. For details, see text. Fig. 323. The origin and distributional history of the Ypthimini (Old World) and Euptychiini (New World). See text for details.

Ypthimini-sect.
Satyrini-sect. & Satyrinae
elymniine ancestor
Hypocystini
?
Ragadiinae

322

to Euptychiini

Callerebia series
Ypthimini
Ypthima series

Euptychiini
radiation

Melampias
series
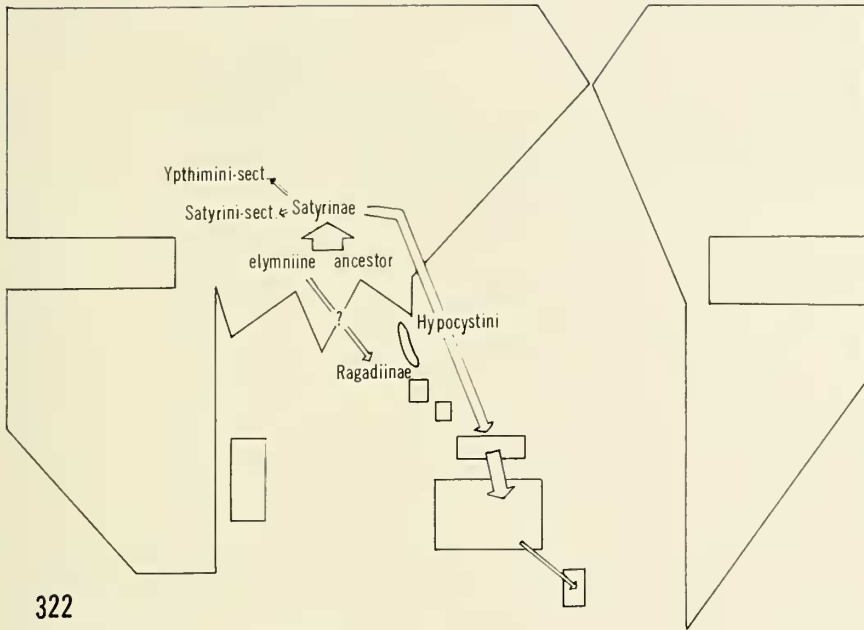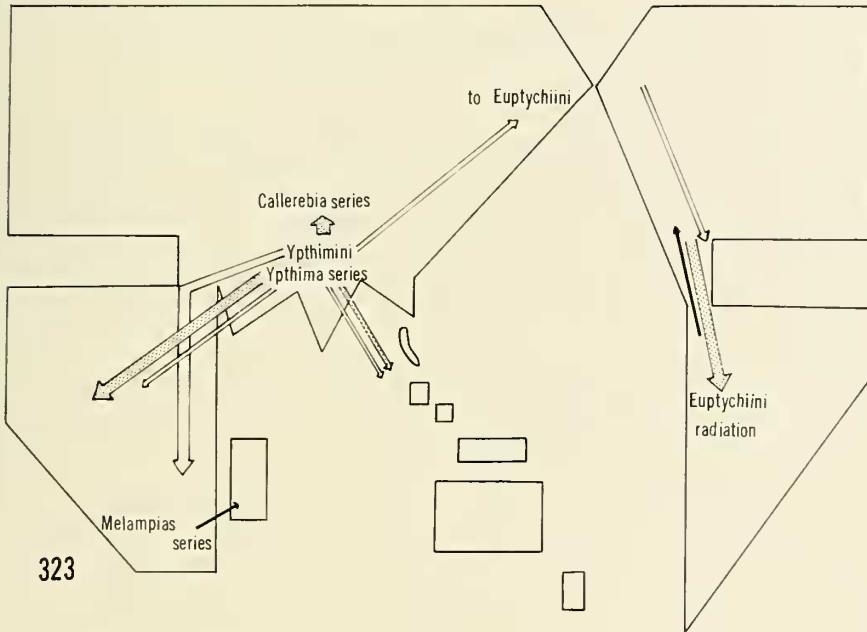
323
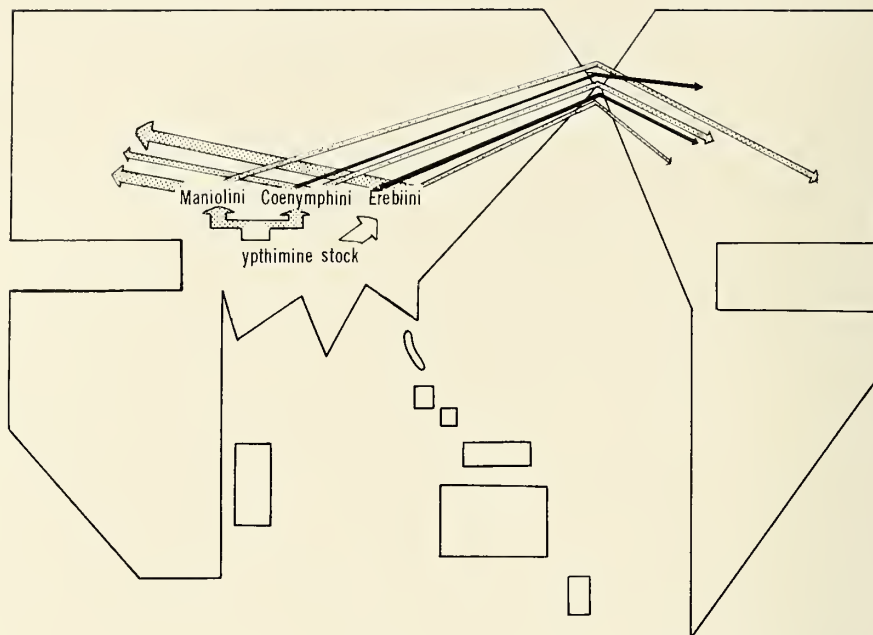
Fig. 324. The origin and distributional history of the Coenonymphini, Maniolini and Erebiini. See text for details.

nophilini and Euptychiini feed as larvae predominantly on Gramineae, which are probably not used extensively by the primitive species.

Just before and during the Pleistocene there was an exchange of faunal elements between the Nearctic and the Palearctic, resulting in such Holarctic distributions as those of *Coenonympha* (Fig. 324), *Oeneis* (Fig. 326) and *Erebia* (Fig. 324), although these genera probably differentiated much earlier, and some of the Holarctic members of the Maniolini (Fig. 324) and Satyrini (Fig. 326).

A proposed phylogeny for the Satyridae is presented in Fig. 327, embodying the information given above.

DERIVATION OF THE SATYRID FAUNAE OF THE WORLD

Comparisons of the faunal compositions of various parts of the world often prove valuable in determining the derivation of the elements of some areas. With this assumption in mind Table 7 was drawn to show the composition by tribes of the Satyridae in major faunal regions of the world.
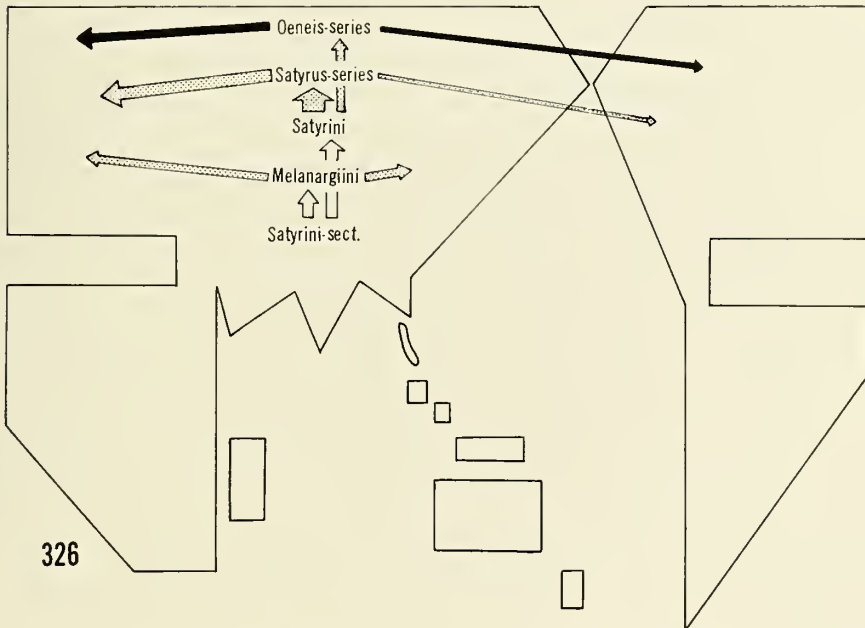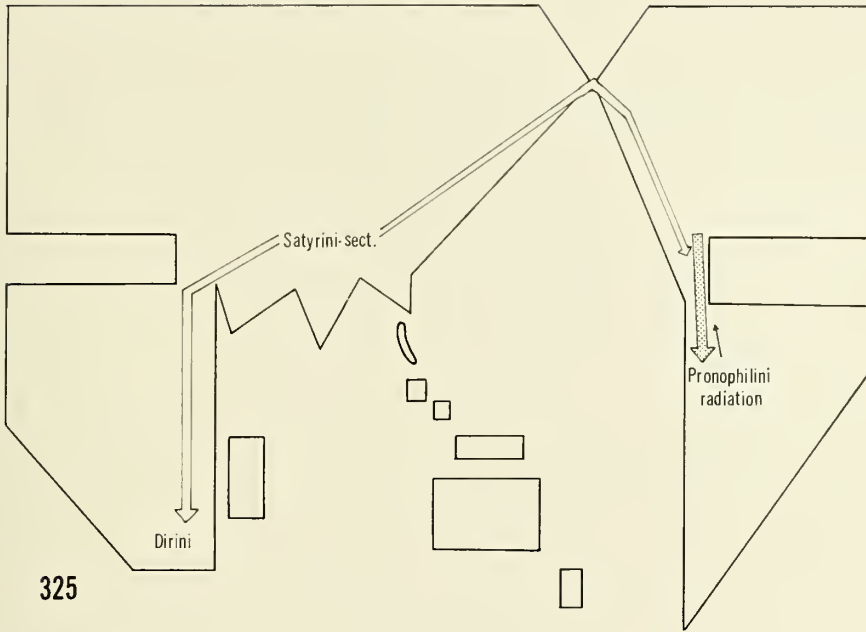
Figs. 325, 326. Fig. 325. The origin and distributional history of the Dirini and Pronophilini. See text for details. Fig. 326. The origin and distributional history of the Satyrini and Melanargiini. See text for details.
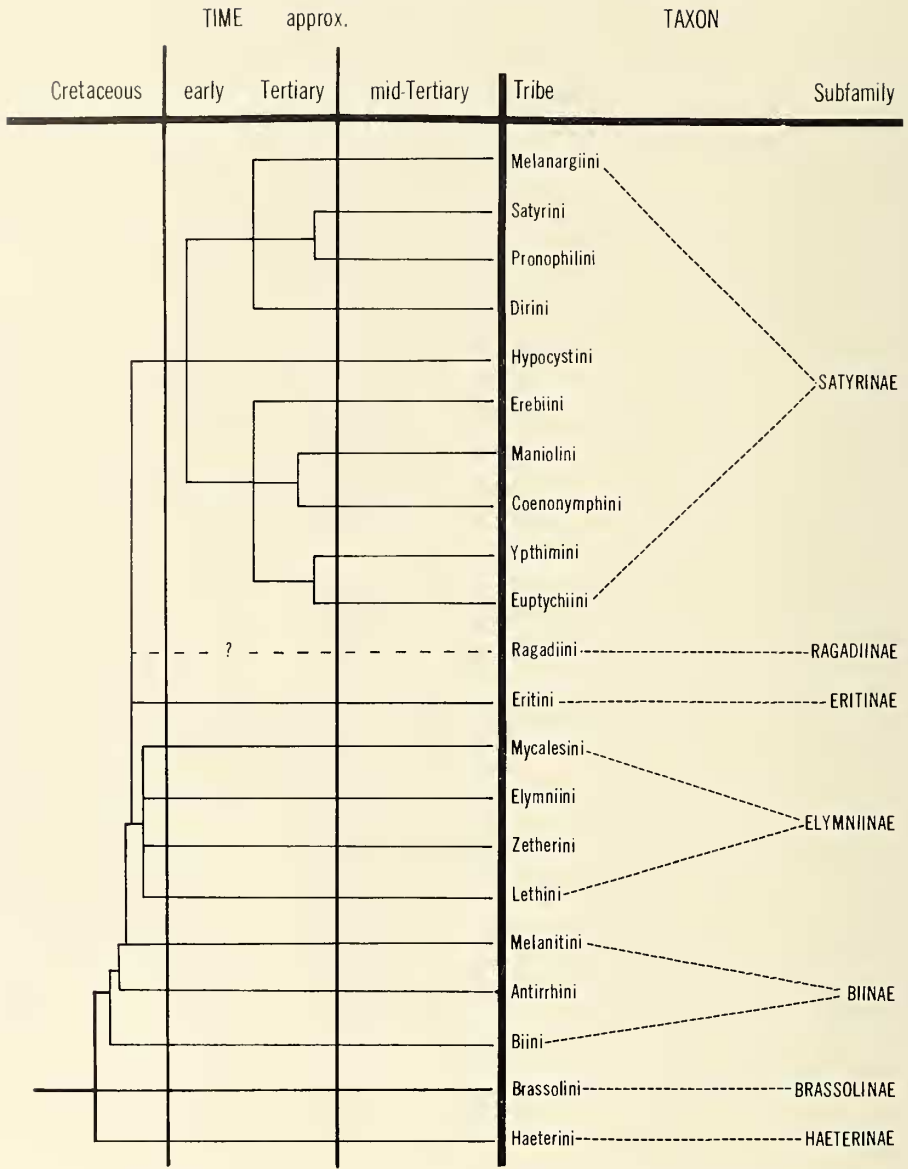
Fig. 327. A proposed phylogeny of the Satyridae showing the relationships of the tribes. The time scales are *very* approximate and conform to the hypotheses proposed in the section on evolution and zoogeography. For details, see text.

The Neotropics.—The Neotropics, as broadly and somewhat incorrectly defined to include Antarctic, temperate and tropical regions of South America, show a satyrid fauna composed of six tribes which are members of four subfamilies. Five of these tribes are endemic, and four of them—Haeterini, Brassolini, Antirrhini and Biini—are the most primitive in the family. The fifth endemic tribe, the Pronophilini, is a member of the Satyrinae and most closely related to the Holarctic Satyrini. The pronophilines probably reached, during the mid-Tertiary, South America and proliferated there. The Euptychiini are exclusively American satyrids most closely allied to the Ypthimini. They were probably derived from a common stock with the Ypthimini, introduced into the Neotropics and proliferated there contemporaneous with the Pronophilini. The euptychiines, while entirely American and overwhelmingly Neotropical, cannot be considered an endemic tribe because seven species are found in the Nearctic, as far north as southern Canada.

In summary the Neotropical satyrid fauna appears to have been derived from two sources. The Haeterinae, Brassolinae, Antirrhini and Biini evolved in tropical America from the basic satyrid stock which either arose in tropical America from a basic nymphaloid stock that was already there or evolved from such a stock that invaded tropical America during the Cretaceous. The Neotropics were then reinvaded, probably in the Oligocene, perhaps even in the Eocene, by two basically Paleotropical groups, the Pronophilini (derived from a Satyrini-section stock) and the Euptychiini (from a Ypthimini-section stock). There has been no extensive immigration in recent times from the Nearctic; indeed, most recent movement in the Americas of the Satyridae has been northward from the Neotropics.

The Nearctic.—The Nearctic fauna has been derived primarily from the Neotropics and the Palearctic. Seven tribes are represented in North America, none endemic, and most species are very recent arrivals, many during the Pleistocene. By far the majority of the species in the Nearctic are assignable to Holarctic tribes or genera. A few of these, such as *Neominois ridinsii, Enodia portlandia* and *creola, Satyrodes eurydice, Coenonympha haydenii* and *Cercyonis* species, appear to be pre-Pleistocene arrivals; these butterflies probably arrived in North America in the Miocene or Pliocene, perhaps even earlier. The remainder of the genera arriving from the Palearctic —*Oeneis,* most *Coenonympha, Erebia*—belong to a basically arctic-

TABLE 7

The taxonomic composition of the world satyrid fauna. a= single species; b = 2 to 5 species; c = 5 to 10 species; d = more than 10 species).

Taxon	Neotropic	Nearctic	E. Palearctic	W. Palearctic	Indo-Malayan	Australian	Trop. Africa	Temp. Africa	Madagascar
Haeterinae	d								
Brassolinae	d								
Biinae	d		a		d	a	c	b	b
Antirrhini	d								
Biini	a								
Melanitini			a		d	a	c	b	b
Manataria	b								
Elymniinae		b	d	c	d	d	d	d	d
Lethini		b	d	c	d		a	b	
Zetherini			a		b				
Elymniini					d	b	b	b	a
Mycalesini			c		d	d	d	c	d
Eritinae					b				
Ragadiinae			b		c				
Satyrinae	d	d	d	d	d	d	d	d	a
Hypocystini						d			
Ypthimini			d	b	d	b	d	d	a
Palaeonympha			a						
Euptychiini	d	c							
Coenonymphini		b	d	d					
Maniolini		b	d	d					
Erebiini		c	d	d					
Dirini								c	
Pronophilini	d	a							
Satyrini		d	d	d	b				
Melanargiini			d	d					
Endemic tribes	5	0	1		2	1	0	1	0

alpine fauna and probably date from the Pleistocene: *Coenonympha mixturata* found in the bogs of Alaska and the Yukon is virtually inseparable from the Siberian population and must be a post-Pleistocene immigrant. The tribes derived from the Palearctic are the Lethini, Coenonymphini, Maniolini, Erebiini and Satyrini. Two

tribes, the Pronophilini and Euptychiini, have entered the Nearctic from the Neotropics. The first of these tribes is represented by a single species, *Gyrocheilus patrobas,* which reaches southern Arizona. This invasion is probably of rather recent origin, perhaps post-Pleistocene, though it is difficult to assign dates to an invasion of a single species. The Euptychiini have left several species in North America, and one group—the *Megisto cymela* complex—has become rather distinct from its Neotropical progenitors. The *cymela*-group probably arrived well before the Pleistocene, whereas the other species in the Euptychiini are closely allied to tropical members and may have arrived during an interglacial.

The Palearctic.—The importance of the Palearctic, while it was not the place of the origin of the Satyridae, nevertheless cannot be overstressed with respect to subsequent evolution. Eleven tribes, representing four subfamilies, are found in this region, although the "true" Palearctic fauna is composed only of the Elymniinae and the Satyrinae. The other two subfamilies, the Biinae and the Ragadiinae, enter the Palearctic only in its southeastern part, were derived from the Indo-Malayan region and need be mentioned only in passing. The Elymniinae are represented by the tribes Lethini, Zetherini and Mycalesini—the last two being found just in the southeastern part of the area and also properly are part of the Indo-Malayan fauna. The tribe Lethini is represented chiefly by the *Pararge*-series—more boreal in its distribution than other lethine groups—which probably evolved in the mid-Tertiary and became cold-adapted. The interesting link between the Lethini and Mycalesini, *Mandarinia regalis,* is found in temperate China, suggesting that the latter tribe may once have been found much farther north than it is today.

The Palearctic is the metropolis of most of the tribes of the Satyrinae, with six represented. Five of these tribes—Satyrini, Melanargiini, Coenonymphini, Maniolini and Erebiini—probably arose in the Palearctic itself in response to progressive drying, with the increase of grasslands, during the early Tertiary. Only the Melanargiini are truly endemic, all other tribes having expanded into the Nearctic during the later Tertiary or Quaternary. The sixth satyrine tribe, the Ypthimini, is primarily Paleotropical, and the Palearctic ypthimines must have been derived from the tribes. One group within the ypthimines, the *Callerebia*-series, is exclusively Palearctic and probably arose from the ypthimine stem about the same time as the

other tribes mentioned above. All members of the *Callerebia*-series now are found under the stringent ecological conditions of the central Asian mountains; none has invaded the main part of the region.

In sharp contrast with the Nearctic, the Palearctic has been very important in the later evolution of the Satyridae. Just why the Palearctic should have played such a role in the evolution of the Satyrinae is a puzzle: there were certainly vast savannas in the Nearctic during the Tertiary (Darlington, 1957), which proved to be the route of dispersal of the forerunners of the Pronophilini and Euptychiini and thus must have been occupied during the Tertiary. The primitive forms of the five Holarctic satyrine tribes are all Palearctic, not Nearctic. The evidence for these tribes having arisen in the Old World is overwhelming. The only tribe which is a candidate for arising in part in the Nearctic is the Satyrini: *Neominois ridingsii* is a rather primitive species, most nearly related to the Asian *Karanasa*. The great proliferation of the *Satyrus*-series (Satyrini) in central Asia argues strongly for its being considered the "birthplace" of the tribe. In all fairness, however, it must be pointed out that North America was the place of the greatest Tertiary development of the horses and camels (Darlington, 1957: 352-354), yet no native species of either group is presently found in North America. Such an evolutionary pattern may explain the satyrids—evolution of some stocks in the New World, spread of these stocks into the Old World, extinction of the Nearctic fauna and reinvasion and repopulation of the Nearctic by Palearctic groups. In the absence of a fossil record, I must accept the neontological evidence that the satyrine tribes evolved in the areas of their present greatest density and diversity. Parallels exist: Simpson (1953: 51-52) mentions the New World oreodonts and pronghorn "antelopes" and the Old World giraffes. None of these groups left the hemisphere of their origin.

The Indo-Malayan region.—This area, bounded roughly by India, the Philippines and Wallace's line, has been likened to the "Garden of Eden" by generations of zoogeographers. Its satyrid fauna is strong only in moderately primitive groups. In all, nine tribes of five subfamilies are represented in the Indo-Malayan fauna. This is the area of the best development of the Ragadiinae and Eritinae, and these are to be considered truly endemic to the region. The melanitines (Biinae) are best represented in the Indo-Malayan fauna and probably arose there or arrived at an early date.

The Elymniinae have reached their highest development in this region, where the four tribes are best represented; all probably arose there. Those genera tending to connect tribes, with the exception of *Mandarinia,* are found on the Malay Peninsula. The bifurcation of the Mycalesini into naked and hairy eyed species took place in this region, and both groups are still found throughout the Indo-Malayan region. These have spread and provide some rather interesting data in the analysis of the African-Malgache fauna. Certain considerations, outlined in the systematic revision, led to the conclusion that the Lethini are the most primitive elymniines. Most lethines have hairy eyes, and for this reason the hairy-eyed condition is considered primitive in the Mycalesini (see also the discussion under the Malgache fauna, which follows).

The Satyrinae are represented by two tribes, the Satyrini and Ypthimini. The former is a secondary immigrant from the Palearctic, only entering the Indo-Malayan region along its northern end. The Ypthimini, however, probably arose in this region and apparently replaced its immediate relatives—forms closer to the present-day *Hypocysta*-series (Hypocystini), which is now restricted to the Australian region east of Wallace's line. The ypthimines spread during the early Tertiary into Africa and the New World, giving rise to the Euptychiini of the latter region.

In summary, due to the prevalence of the Melanitini, Elymniinae and intermediate genera in this region, the Indo-Malayan region is considered to have given rise to the elymniines. The Eritinae and Ragadiinae also arose in this area. The Indo-Malayan region did not play an important role in the later evolution of the Satyrinae: the focus of that subfamily shifted to the Palearctic.

The Australian Region (including the Pacific Islands).—Faunistically the Australian region, including Australia, New Guinea, New Zealand and the nearby islands, is one of the most interesting. It is distantly related to the Indo-Malayan region, but substantial interchange of faunal elements between these regions occurred only in the distant past. Simpson (1961b: 443) has dated the extensive immigration of the marsupials into Australia as Cretaceous or Paleocene, and it was probably at that time that much of the regional butterfly fauna arrived. Elsewhere Simpson (1961b: 435-436) shows that several waves of rodent groups arrived in the Australian region from

the Indo-Malayan from Miocene time to the present. All the tribes represented in the Australian region have also penetrated the Pacific islands, over water, hence the islands are considered along with the continent.

Just one tribe is endemic in this region, the Hypocystini. The metropolis of the *Xenica*-series is Australia, with some aberrant species in New Zealand. All the satyrids in New Zealand were derived long ago from the Australian ones. The *Hypocysta*-series is best developed in New Guinea and has spread into the Pacific islands. The other satyrine tribe represented in this region is the Ypthimini, the members of which are highly modified, particularly the Pacific island genus *Xois*. The Ypthimini, as shown by their expansion into Africa and the Americas, was a fairly plastic group.

A single *Melanitis* is found throughout the region in question, *M. leda*, a widespread species distributed west to the westernmost part of Africa. The same may be said about those Elymniini which occur on these islands; all are widespread species. The arrival of *Melanitis* and *Elymnias* must have been a recent event since they are little differentiated from their continental progenitors. The Mycalesini of the region reflect the probably early spread of this tribe, since it also reached Madagascar.

In summary, the satyrid fauna of the Australian region was derived from the Indo-Malayan region, and this derivation very early, resulting in a highly distinctive fauna. If the time schedule for the marsupials is valid for the satyrids, most of the groups reached the region in late Cretaceous to earliest Tertiary times. This indicates that the Hypocystini of the most evolved subfamily, Satyrinae, were in existence by the earliest Tertiary. A few strong flying species, such as *M. leda*, probably arrived over water very recently.

The Ethiopian Region.—This region includes both the tropical part of Africa and temperate South Africa. These are faunistically very different areas, but they are so intimately related that they must be considered together.

There is a single endemic African satyrid tribe, the Dirini. This tribe, which has morphological affinities with both the Elymniinae and the Satyrini-section of the Satyrinae, is restricted to South Africa. Several interpretations are possible for the Dirini: (1) the Satyrinae arose in Africa, (2) the Dirini were exterminated in all places but

South Africa or (3) the Dirini stock was isolated in South Africa with the expansion of the tropical rainforest belt into eastern Africa, and it evolved there. The first alternative is highly improbable, as I have shown in the discussion of the Hypocystini in the systematic revision, but either (2) or (3) might be possible. In the absence of a fossil record we shall never really know. The only other tribe of the Satyrinae represented in the African fauna is the Ypthimini. The ypthimines of tropical Africa are closely related to the Indo-Malayan ones, whereas most of the South African ypthimines belong to the more or less endemic *Melampias*-series, one member of which is also found on Madagascar. It seems likely that the *Melampias*-series were early invaders of Africa—contemporaneous with the invasion of the Dirini—which differentiated and were then forced south and were replaced in tropical Africa by the ypthimines that arrived later.

The Lethini show a similar pattern. In southern Africa two very primitive lethines, the *Aeropetes*-series, are found which probably are remnants of an early fauna. The East and South African genus *Aphysoneura* is much more like the Indo-Malayan lethines, and it was probably a later faunal addition. The Mycalesini have made a significant invasion of Africa. All the species on the continent have naked eyes, unlike those on Madagascar, and probably represent a later immigration, contemporaneous with the arrival of the "conventional" ypthimines and *Aphysoneura*. The mycalesines will be considered in further detail in the discussion of the fauna of Madagascar. The elymniines and the melanitines of Africa are representatives of the most widespread groups and almost certainly arrived from the Indo-Malayan region, probably fairly recently: frequently the African members are conspecific with their Indo-Malayan counterparts.

In summary, Africa appears to have been populated more than once from the Indo-Malayan region. The tropical African satyrid fauna looks more like a depauperate Indo-Malayan fauna than anything else, but that of temperate Africa has evolved significantly and is quite distinct. Probably the South African endemic groups represent the "old" African fauna of the early Tertiary, whereas that of tropical Africa is younger, perhaps dating from the Oligocene or even the Miocene (Darlington, 1957: 590). Such species as *Melanitis leda* probably arrived in tropical Africa much more recently.

Madagascar.—There can be little doubt that the colonization of
Madagascar was from Africa, but mostly so long ago that the species
bear little resemblance to species now found on continental Africa.
The Melanitini and the Elymniini of this island, on the other hand,
are conspecific with their mainland counterparts, as is the only mem-
ber of the Satyrinae, a species of Ypthimini: all these butterflies are
probably recent introductions, no doubt by waif dispersal.

The most interesting satyrids in Madagascar, from a zoogeo-
graphic standpoint, are the Mycalesini—the dominant tribe on the
island. As noted before, both naked- and hairy-eyed mycalesines
occur in the Indo-Malayan regions, whereas those from continental
Africa have naked eyes. The species found in Madagascar, without
exception, have hairy eyes. One would be tempted at first glance to
postulate that the Malgache mycalesines were derived directly from
the Indo-Malayan ones. This is precisely why the mythical continent
of "Lemuria" was postulated: a land bridge to account for the similar
Malgache and Indo-Malayan lemurs; the Madagascar genera are less
like continental African genera than any of the continental genera
are like each other. In the mycalesines, dissimilarities indicate a long
isolation of the Malgache fauna. For this reason it seems more
likely that the mycalesines migrated into Africa very early (Creta-
ceous or Paleocene?), and that stock which made the first immigra-
tion was hairy-eyed, as is characteristic of primitive elymniines. Fur-
thermore, the Malgache mycalesines have a less clubbed female
foretarsus than do the continental species. These mycalesines were
contemporaneous with the Dirini, *Melampias*-series of the Ypthimini
and the *Aeropetes*-series of the Lethini and formed part of the "old"
African satyrid fauna. Madagascar received its mycalesine fauna
from this very early invasion. Just when this occurred is problematic:
Matthew (1915: 204-205) thought that Madagascar and Africa
were never physically connected, and Darlington (1957: 535) be-
lieved that the Malgache fauna may have begun to accumulate in the
Oligocene. In any event, the Malgache mycalesine fauna is probably
of early Tertiary age. Climatic changes or pressure of competition by
the later mycalesine immigrants—which did not reach Madagascar—
replaced the hairy-eyed mycalesines on mainland Africa, leaving the
morphologically primitive Malgache fauna completely isolated geo-

graphically from their nearest relatives in the Indo-Malayan region. Such invasion and subsequent extermination of geographically intermediate populations is well known among fossil vertebrates (Darlington, 1957: 102-121; 159-172; 206-230).

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